Selection and Performance of Ecosystem Attributes for Assessment of Restoration Success in Biodiversity Offset Models

---

A thesis submitted in partial fulfilment
of the requirements for the Degree
of
Doctor of Philosophy
in Forest Sciences
by

Constanze Keye

School of Forestry
University of Canterbury
2017

Table of Contents

List of Figures

List of Tables

Abstract

Biodiversity offsets are an international emerging impact assessment tool, attempting to bridge the gap between biodiversity conservation and sustainable economic development. Offsets shall compensate for unavoidable ecological damage after appropriate prevention and mitigation measures have been taken so that there is no net loss and ultimately a net gain for biodiversity near the impact site. Worldwide, ecologists are being challenged in choosing the most appropriate ecosystem attributes for use in biodiversity offset models. Attributes ought to represent the key biodiversity features at a given site, be quantifiable, easy to measure, reliable, and sensitive to management actions. However, biodiversity is complex and not easy to describe or measure, especially in the context of offsetting. Determining which attributes are the most appropriate for this task is currently compromised by the lack of a theoretical framework. To ensure that offsetting does result in genuine biodiversity retention, attribute choice has to be based on a sound scientific basis.

To help establish such a foundation, this thesis first suggests a conceptual framework for attribute selection in forest ecosystems. Then ecosystem attributes commonly applied or suggested for the assessment of restoration success in forests are reviewed and a set that appears to be most suitable for application in biodiversity offsets is identified. Second, the performance of vegetation related attributes in terms of their predictability and information content are tested in a New Zealand restoration project using a chronosequence approach. Third, the surrogacy value of these vegetation measures for other species groups and ecosystem function is assessed. In particular, how well the recovery of aboveground attributes can predict the restoration of belowground attributes is assessed. This is critical, as typically the largest amount of site biodiversity occurs below-ground. Finally, a general set of attributes that will be applicable in most forest types is identified for biodiversity offset models. In addition, further recommendations for attribute selection within offsets models and how to manage uncertainty associated with them are given.

Results of this thesis suggest that: (i) Structural elements such as basal area and mean diameter are the most predictable attributes, providing important information about the successional development of forests. (ii) Compositional measures can be less predictable but provide the highest information content.

Predictability of these measures can be optimised if early to mid-successional stages are used as a restoration target and if restoration includes active management such as planting. (iii) Vegetation measures do not correlate well with the recovery of belowground species groups, but further research is necessary to confirm this. (iv) This research emphasises that the re-creation of old growth forest attributes can take several centuries when starting from early successional stages. It might be also surrounded by a high uncertainty in respect to compositional development; in particular, when passive reestablishment of vegetation is applied as a restoration tool. Therefore, achieving a no net loss of biodiversity as required by biodiversity offsets might, in many cases, be doubtful when offsetting for the loss of old growth forest habitats.

Acknowledgements

There are a great many people who made this thesis possible. But the foremost thanks has to go to Christian Roschak who consistently supported and encouraged me, especially at times where the PhD road was rocky and winding and felt like the way to Mount Doom. Without his tireless assistance during field work and the endless hours he spent helping me to prepare field material, this thesis would still not been finished.

I have to thank my main supervisor David Norton for providing timely support and feedback. I'm also thankful to my co-supervisor Tara Murray who spent long evenings in the lab bringing me up to speed on basic entomological knowledge and provided valuable feedback. I'm grateful to Graham Ussher and Bruce Burns for their involvement in developing the PhD proposal. Thanks, Graham, for taking your time to show me the restoration work at Tiritiri Matangi.

I am profoundly grateful to Hugh Wilson for providing in depth botanical guidance on the fascinating New Zealand plant world and sharing his comprehensive knowledge about all aspects of Hinewai Reserve with me. Hugh, thanks for being so continuously cheerful, possessing such a great sense of humor, and always having time for a cup of tea!

Without the self-made Tullgren funnels from Steve Pawson, the invertebrate study would not have been possible. I'm particularly in debt to Peter Johns who spent days tirelessly identifying and rechecking my invertebrate classification, putting up with my non-entomological background, and correcting me patiently (all mistakes are mine alone). Leo Coldron provided valuable guidance and advice on the soil aspects of my work. I further like to thank the following people for their assistance, feedback or advice: Alan Leckie, Luis Apiolaza, Chris Green, Barbara Barratt, Hunter Harrill, Jess Furlong, Graeme Ure, and Cecilia Casnati. Finally, I would like to acknowledge the generous financial support received from the University of Canterbury (UC Women in Engineering Scholarship 2011–2014, Owen Browning Scholarships in Forestry 2015) and the School of Forestry. The Brian Mason Trust kindly provided funding for soil related aspects of Chapter 6. Last but not least – without the perfectly roasted coffee beans from Nigel Pink this thesis would never have been finished. Thanks, Pinks Elixir you kept me wide awake!

Chapter 1
Introduction

1.1. *The Worldwide Loss of Biodiversity*

The world is currently witnessing an unprecedented loss of biodiversity (May 2002; McShane et al. 2011; Secretariat of the Convention on Biological Diversity (CBD) 2005). The rate of species loss is such that the term *sixth mass extinction* is widely used in the literature (Magurran 2005; Wake & Vredenburg 2008). Concerned by this loss, the United Nations in 1992 prepared the most significant international treaty for the conservation and sustainable use of biodiversity: the Convention on Biological Diversity. It also introduced one of the most commonly used biodiversity definitions (United Nations Environment Programme 1992):

> "*'Biological diversity' means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic systems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.*"

The treaty was signed on 5th June 1992 by more than 150 countries at the United Nations Conference on Environment and Development in Rio de Janeiro. One important objective of the treaty, set subsequently in 2002 at the Sixth COP[1], was to slow down the loss of biodiversity by the year 2010 significantly. A recent evaluation showed that this ambiguous aim was not achieved (Leadley et al. 2010; UNEP 2007). The short time period set and the difficulties in measuring and monitoring such a complex and unequally understood construct as biodiversity on a worldwide scale impeded meeting this goal (Barbault 2011). However, the main reason was that management actions carried out to address species loss rarely focused on the underlying causes (Secretariat of the Convention on Biological Diversity 2010; UNEP 2007). The "evil quartet" (Diamond 1989) of overkill, habitat destruction, chains of extinction, and introduced species have not only persisted but worsened over the last 10 years (Butchart et al. 2010), leading to further extinctions and subsequent biodiversity loss. All these causes are rooted in unsustainable resource use (UNEP 2007). Therefore, the sixth mass extinction is the first mass extinction caused by a single species, known as *Homo sapiens* (Magurran 2005).

[1] COP = Conference of the Parties to the Convention on Biological Diversity

Over 7 billion people currently live on earth, with no end in sight to population growth in the near future (Tollefson 2011). Thus, the pressure on natural resources will further increase leading to even more habitat destruction and degradation. The traditional approach of conservationists, the establishment of protected areas, will remain a key strategy for biodiversity protection. However, only about 13 % of the terrestrial landmass is currently protected inside conservation areas (United Nations 2011), accompanied often by an uncertain outcome for biodiversity protection and severe problems for local people (Mulongoy & Chape 2004). Protected areas mainly cover ecosystems that are still in a reasonable natural condition. Thus, only one goal of large-scale biodiversity conservation, the protection of ecosystems in a semi-natural condition, can be achieved (Hunter, 1999). The other important part of biodiversity conservation, the restoration of significantly degraded ecosystems, is mostly confined to the unprotected part of the earth's surface. Hence, the establishment of protected areas alone will not stop the loss of biodiversity (Roe & Hollands 2004). The growing human population demands more energy, fibre, food, and space. Thus, it will become more and more difficult to lock areas away in perpetuity (Leadley et al. 2010).

1.2. *The Situation of Biodiversity in New Zealand Forests*

Due to its long period of isolation from the rest of the world, New Zealand experienced an exclusive evolution resulting in a unique biodiversity. As a result, the majority of species across several taxonomic groups are endemic to New Zealand; they cannot be found anywhere else in the world. For example, about 80 % of vascular plants (excluding mosses and liverworts) and 87 % of all terrestrial bird species are endemic to New Zealand (Ministry for the Environment & Department of Conservation 2000). As a result, New Zealand was identified as one of 25 biodiversity 'hotspots' in the world, requiring top conservation priority (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). Myers at al. (2000) define biodiversity hotspots as regions containing more than 0.5 % of the world's endemic plants and which have lost 70 % or more of their primary vegetation cover. What are the reasons for New Zealand experiencing one of the most rapid losses in biodiversity on earth? Once more, the "evil quartet" (overkill, habitat destruction, chains of extinction, introduced species) have been heavily involved, especially in New Zealand's forest ecosystems. Before the arrival of humans, New Zealand was almost completely dominated by forest (McGlone, 1989).

Colonisation of New Zealand by Polynesians and later Europeans was the key driver for the destruction of large areas of primary forests. The cultivation of land by Europeans was accompanied by burning of large areas of forest to enable the establishment of farmland, exotic forests, and human settlements. These actions have led to a decrease of indigenous forest cover by nearly three-quarters during the past 750 years (Fleet, 1986). The remaining forests, although covering about 23 % of New Zealand's landmass, are unrepresentative of their pre-human distribution, being now biased towards uplands and higher rainfall areas. (Leathwick et al. 2003; Norton & Miller 2000). In much of lowland New Zealand, only isolated remnants persist from the once widespread forests due to the high value of lowland environments for production activities (Norton, 2000). While human land use decisions are still likely to be the most pervasive threat to terrestrial indigenous biodiversity; a significant peril arises today from introduced species, especially browsing and predatory mammals (Allen & Lee, 2006; Saunders & Norton, 2001). Introduced species can cause major impacts on indigenous ecosystems. For example, predation on native bird species or heavy browsing on selected plant species can result not only in degradation but also in irreversible changes in ecosystem composition and structure (Norton 2009b; D. A. Wardle et al. 2001). Furthermore, the impact of introduced species persist today and forests can still be easily converted into pasture on private land; hence it is important not to view the current extent or condition of especially lowland indigenous forest as permanent. The destruction and degradation of forests have contributed to a massive decrease in New Zealand's unique biodiversity.

1.2.1. New Zealand's Biodiversity Policy

Around 33.4 % of the terrestrial New Zealand land area is currently protected for biodiversity conservation. These protected areas contain three-quarters (46,250 km²) of the remaining indigenous forests in New Zealand. These forests are Crown owned and largely protected from clearance and development through administration by the Department of Conservation (Ewers et al., 2006). Notwithstanding this protection, biodiversity decline has continued in New Zealand. The New Zealand Biodiversity Strategy[2] (NZBS) (Ministry for the Environment & Department of Conservation 2000) concluded that biodiversity loss cannot be stopped by the establishment of protected areas alone, as pressures on biodiversity even inside protected areas, especially the effects of

[2] The New Zealand Biodiversity Strategy represents the ratification of the Convention on Biological Diversity in New Zealand.

introduced organisms, continue. Furthermore, some native biodiversity is largely or entirely dependent on private land. This is caused by the biased distribution of protected areas towards economically less important mountainous environments (Ministry for the Environment 2011). As mentioned above, the smallest proportions of protected forests are lowland forests. Consequently, specific key objectives of the NZBS are to maintain and restore biodiversity values outside of conservation areas and to restore biodiversity values within protected areas. The overall aim is, in consistency with the aim of the Convention on Biological Diversity, to halt the decline of New Zealand's indigenous biodiversity. In contrast to the sixth COP[3] resolution, the New Zealand goal is to halt the decline of biodiversity by 2020, not by 2010. To further support these objectives and to especially address the threat which biodiversity values are facing on private land, the Proposed National Policy Statement On Indigenous Biodiversity (NPS) was developed (Ministry for the Environment 2011). The NPS outlines the importance of protecting significant indigenous vegetation and habitats of indigenous fauna on private land. However, pressure on private and public land is increasing and will increase more so with the growing human population which will require new resources and infrastructure, like wind farms and landfills (Department of Conservation, 2010). This situation is not unique to New Zealand and solutions have to be found worldwide to merge development actions, sustainable resource use, and biodiversity restoration outside of protected areas. One possible solution is to use tools that address the ecological impacts of developments by effectively placing an economic value on biodiversity (Nijkamp et al. 2008). One of these instruments is the so-called "biodiversity offset" which is investigated in this thesis.

1.3. *Biodiversity Offsets*

The negative effect of development projects on biodiversity is widely recognised (Treweek 1999). Therefore, tools like the 'mitigation hierarchy' are commonly applied in environmental impact assessment. The mitigation hierarchy seeks to avoid, minimise, and mitigate harm to biodiversity. However, even if the full range of the mitigation hierarchy is applied, negative adverse effects, and with that a net loss of biodiversity, often remains at the project site. This is usually because not every impact on biodiversity can be mitigated by on-site restoration actions. One approach to compensate these residual effects is financial payments

[3] COP = Conference of the Parties to the Convention on Biological Diversity

or off-site conservation activities by developers (Madsen et al. 2010). This form of compensation is likely to result in a net loss of biodiversity; as it does not explicitly quantify and compare the biodiversity lost at the impact site with the biodiversity gained by the conservation project.

In the past, this net loss of biodiversity was often considered acceptable and perhaps unavoidable. In recent years, the inevitability of this outcome has been questioned, leading to the development of a tool that is currently emerging within international compensation practice: the biodiversity offset (ten Kate et al. 2004). Offsets seek to compensate for unavoidable ecological damage caused by development projects after appropriate prevention and mitigation measures have been taken. The overall offset aim being to achieve a no net loss and ultimately a net gain, for biodiversity near the impact site (ten Kate et al. 2004). What differentiates biodiversity offsets from other tools for managing development impacts is that associated biodiversity losses are explicitly quantified, as are the gains that are proposed to arise from the offset. (BBOP 2009b).

Two main types of biodiversity offsets are distinguished: (i) removing threats to a site caused by continuing or expected development impacts (averted loss offsets) or (ii) enhancing already degraded habitat i.e. restoration projects (Maron et al. 2012). Enhancement offsets might either further protect or restore areas that already hold significant conservation value by management actions, such as removal or control of introduced predators or herbivores (Norton 2009a) but are not further discussed here. Alternatively, new habitats can be created through active (plantings) or passive (facilitation of natural succession) restoration techniques in order to balance for biodiversity loss from the impact site (Moilanen et al., 2009). The concept of biodiversity offsetting is currently being investigated internationally through the Business and Biodiversity Offsets Programme (BBOP). However, there are still many conceptual and methodological challenges surrounding their successful application (Kiesecker et al. 2009; Maron et al. 2016). Key issues include ethical concerns associated with trading biodiversity values, determining which aspects of biodiversity are most important for the society, and the more technical challenges of how to effectively and transparently quantify biodiversity loss and gain (Maron et al. 2016).

1.3.1. Biodiversity Offset Accounting Models

The required quantification of site biodiversity in offsets is based on measured ecosystem components, called attributes. The selected attributes are thought to be most suitable to represent different aspects of site biodiversity (BBOP 2009b). It has been repeatedly cited (e.g. Maseyk et al. 2016; ten Kate et al. 2004; S. Walker et al. 2009) that they should capture, as Salzman & Ruhl (2000) phrased it: "…what we care about…" of site biodiversity. The condition of the biodiversity at the impact site is assessed prior to the development by examining and comparing attribute values with a reference site (benchmark site). This reference site is most commonly an area of land that provides a habitat in 'good condition', representing the type of biodiversity that will be affected by the development action (BBOP 2009c). It is also necessary to estimate the change in biodiversity condition at the impact site after the development has taken place. The reference site is then used to quantify biodiversity values gained by the planned restoration actions at the offset site; based on the same attributes that have been measured at the other two sites. The selected attributes are then used to calculate the sufficient offset ratio to ensure a no net loss of biodiversity. In addition, they should also be applied in monitoring to ensure model fit after the initial offsetting has occurred (BBOP 2009b). Monitoring will enable adaptive management to ensure restoration success at the offset site and the archival of a de facto "no net loss" of biodiversity (Burgin 2008). A simplified model of the biodiversity offset process is depicted in Figure 1.

The Business and Biodiversity Offset Programme (2009) suggests several methods and currencies[4] to calculate the project outcome for biodiversity, and with that, the required offset ratio. Measures range from simple area exchange rules (e.g. 1 ha:1 ha per habitat type) to more sophisticated approaches, which take the quality of the biodiversity at the impact site into account (Bedward et al. 2009). For example, one accounting model that was developed in Victoria, Australia, and can be found regularly in biodiversity offset literature worldwide, is the habitat hectare approach (e.g. Anglo Platinum, 2009; Berner, Dickson, & Andrianarimisa, 2009; City of Bainbridge Island, 2009). The habitat hectare method employs an index of affected area size, in combination with site biodiversity condition, to calculate biodiversity losses and gains (Parkes et al. 2003).

[4] According to BBOP (2009c) currencies (or metrics) are the unitary measures of biodiversity lost, gained or exchanged at the impact and offset site.

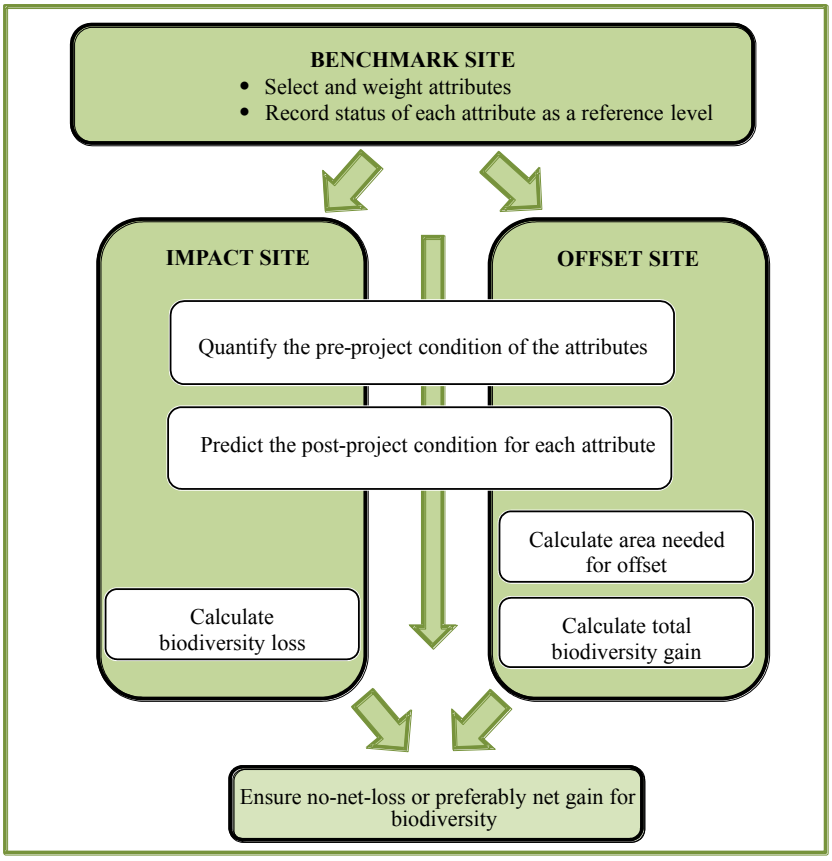


Figure 1. Development stages of a simplified biodiversity offset model.

The simplified offset model in Table 1 is used to illustrate the calculation of biodiversity loss at the impact site. How these calculations are factored into the overall biodiversity offset context is displayed in Figure 1. Calculation for the offset site would be done in the same way. In the example of Table 1, it is assumed that 10 ha is affected by the development process. The site's biodiversity is described by a number of attributes focusing mainly on structure of the affected habitat as a proxy or surrogate for composition and function. In addition, the attributes might be weighted differently dependening on their relative importance to the overall condition of the reference ecosystem (BBOP 2009a).

In the example model (Table 1), three biodiversity attributes have been employed: canopy cover, log density, and large trees. All three represent surrogate measures; deep, multi-layered canopy cover is thought to represent old growth forests, logs are an important source of nutrients and habitat for specialised species, and large trees provide habitat for other specialised species and are again an indicator of forest age (City of Bainbridge Island 2009).

Table 1. A modified biodiversity offset model example from BBOP (2009c) of how to quantify loss at a project impact site using the habitat hectares method.

Total Hectares affected (A)=10	(B)		(C)	(D)	(E)	(F)	(G)	(H)	
Attributes	Benchmark condition		Weighting of the attributes	Pre-project condition	Post-project condition	Pre-project HH/ha	Post-project HH/ha	Net loss of HH/ha	HH lost
	#	Units or Bands				(D/B)*C	(E/B)*C	F-G	H*A
Attribute 1: canopy cover	100%	%	0.3	80%	40%	0.24	0.12	0.12	1.2
Attribute 2: log density	2	logs/ha	0.3	1	0	0.15	0	0.15	1.5
Attribute 3: large trees	20	trees/ha	0.4	10	5	0.8	0.1	0.7	7
		Total:	**1**			**Total habitat hectares lost:**			**9.7**

The condition of the biodiversity at the impact site is assessed by comparing it to the selected reference site. For example, for the attribute 'large trees', 20 trees are given as a benchmark against which the number of large trees at the impact site (i.e. 10 large trees) is measured (Table 1). The habitat hectares are calculated for each key habitat identified. For every biodiversity attribute within this habitat, its condition in relation to the benchmark value is multiplied with the affected area size (Table 1). Finally, the habitat hectares are summed up for all attributes and this gives a measure for the biodiversity that will be lost. It is then usual to identify an offset method to calculate the likely gain at the offset site and compare this with the values calculated for the impact site. The result from this will show if the extent of the offset is sufficient to achieve a no net loss of biodiversity or if the offset measures have to be further increased. A 'modified' habitat hectare method has also been developed further, through the BBOP case studies (2009b), to include not only habitat structure but single species measures as well.

The modified habitat hectare method, just as the other methods suggested by BBOP, requires complex model development (BBOP 2011). Model input variables are biodiversity attributes that are thought to suitably represent the biodiversity present at a specific impact and offset site.

Biodiversity is a complex and broad concept; it is not easy to describe or measure. The mechanisms that support biodiversity are not fully understood and a complete catalogue of all species for even a single forest ecosystem is rarely, if ever, achieved (Hunter 1999). This raises several problems for biodiversity offsetting.

(i) How to determine which attributes are the ones most appropriate for the task of measuring biodiversity values? Currently, there is no theoretical framework at hand to guide the crucial choice of attributes and every project is left to make its own decisions. This may result in a less than ideal approach; to base the offset model entirely on data that is already available, irrespective of the suitability of attributes. In essence, every biodiversity offset represents a restoration project. The question of attribute choice is therefore closely connected to how to calculate and predict restoration success at each individual site. How to draw on this relationship for attribute selection in offset models is explored in Chapter 2.

(ii) The frequent use of vegetation-related attributes (Gardner et al. 2013) as surrogate measures for other unknown or unmeasured aspects of biodiversity (Rodrigues & Brooks 2007). The habitat hectares method is entirely based on this approach (Parkes et al. 2003) and requires the risky assumption that if the measured vegetation attributes are restored, the unknown species they are being used as surrogates for will settle in by themselves (Hilderbrand, Watts, & Randle, 2005). Research over the past decade has shown that this is not necessarily true (Cristescu et al. 2013; Grantham et al. 2010; Murphy et al. 2011). This issue is further addressed in Chapter 6 of this thesis, where vegetation recovery is compared to the restoration of some important belowground measures.

(iii) Temporal delays and uncertainty in the process of gaining biodiversity / conservation value at the compensation site (Moilanen et al. 2009; Vesk et al. 2008). This issue occurs if the new habitat is to be created or if habitat enhancement through predator control is to be undertaken. For the calculation of the total amount of compensation required, it is therefore necessary to predict biodiversity gains as well as associated time frames; i.e., how long it will take until the ecosystem condition has reached the target (reference) values. The estimation of the time lag is of crucial importance in order to determine how much area should be set aside additionally to offset the impact (Moilanen et al. 2009).

1.4. *Thesis Scope and Outline*

The overall objective of this thesis is to support the development of a robust and sustainable system for biodiversity offsetting in forest ecosystems. To overcome the issues that have been identified with biodiversity offsets and to ensure that offsetting does result in genuine biodiversity gains, attribute choice for

biodiversity offsets has to be based on a sound scientific basis. As a step towards establishing this basis, this thesis investigates ecosystem attribute selection and performance for biodiversity offsets in forested ecosystems.

In Chapter 2 a conceptual framework for attribute suitability and selection is developed. The close link between biodiversity offsets and restoration ecology is emphasised and it is concluded that ecosystem attributes are sought that are most suitable to describe restoration success. Ecosystem attributes commonly applied or suggested for the assessment of restoration success are evaluated and a general list of promising attributes is given.

Over the next four chapters, a case study in New Zealand is then used to thoroughly test the suitability of most of these attributes. These chapters address the following key questions:

i. Do attributes change in a predictable way (i.e. do they follow a consistent trajectory over time)?

ii. What is the information content provided by the attribute regarding the assessment of restoration success?

iii. Which attributes show the strongest and most consistent responses towards changes in ecosystem condition?

iv. How effective are vegetation measures as indicators of belowground processes and species groups / biodiversity?

The case study (see next section) uses a chronosequence approach to evaluate attribute development over increasing recovery time. Two main vegetation trajectories on abandoned farmland were followed. Chapter 3 to 5 focus on vegetation related attributes describing composition (Chapter 3), structure (Chapter 4) and biodiversity (Chapter 5) of an ecosystem. Chapter 6 then examines how well the recovery of these vegetation attributes relate to the restoration of belowground measures such as leaf litter invertebrate composition and selected soil parameters.

Finally, Chapter 7 summarizes the findings of preceding chapters, suggesting a set of attributes which will be generally applicable in most forest types for biodiversity offsets. General recommendations for attribute selection for offsets are given and areas for future research are highlighted.

1.5. *The Case Study Area: Hinewai Reserve*

Hinewai Reserve is located in the south-east corner of Banks Peninsula (Figure 2) on New Zealand's South Island (43° 50'S, 173° 02' E). With altitudes between 20 m to 806 m, the climate at Hinewai ranges from cool temperate to subalpine (Wilson 1993). Soils are mostly upland yellow-brown earths derived from loess, free-draining and moderately fertile to fertile (Wilson 1988). Rainfall increases with altitude, with annual means ranging from 1170 mm to 1800 mm (Wilson 1994). Mean monthly rainfall is highest in August (195 mm) and lowest in January (98 mm) at 450 m a.s.l. (pers. comm. Hugh Wilson 20.03.2017, Manager of Hinewai Reserve). The average temperature ranges from 17 °C in January (9 °C – 19 °C) to 7 °C in July (2°C – 8 °C) (D. A. Wardle et al. 2006, pers. comm. Hugh Wilson 20.03.2017).

The private nature reserve is owned and managed by the Maurice White Native Forest Trust. Starting in 1987 with initially 109 ha of former farmland, the reserve is currently 1250 ha, due to several subsequent land purchases. Prior to human settlement most of the upland forest would have been dominated by red beech (*Fuscospora fusca*) and below 300 m by podocarp/broadleaved forest dominated by *Dacrycarpus dacrydioides*, *Prumnopitys taxifolia* and *Podocarpus totara*. The former continuous forest cover was severely reduced between 1850 and the mid-1880s with pasture reaching its greatest extent probably between 1900 and 1930. The whole area was highly altered by logging, burning, spraying, and grazing prior to reservation (see Wilson 1988, 1994, 1998 for more information on the history of Hinewai). Only about 50 ha of old growth forest, mostly dominated by red beech (*Fuscospora fusca*), are left in the reserve. The remaining 1180 ha are in transition between various successional stages from pasture back to forest (Wilson 1994). More than half of the reserve is still covered with invasive plants such as gorse (*Ulex europaeus*) and broom (*Cytisus scoparius*).

The restoration objective of the Trust is to protect and promote native vegetation and wildlife. To achieve this goal Hinewai Reserve is managed according to the "minimum interference strategy" defined by McCracken (1993). Natural succession is promoted by removing any obvious impediments but leaving the succession mostly to itself. The management objective is to interfere as little as possible in the successional sequence. In the sense of this strategy, barriers to natural succession and restoration, in particular introduced herbivorous mammals such as goat (*Capra hircus),* hare (*Lepus europaeus),* possum

(*Trichosurus vulpecula*) and red deer (*Cervus elaphus*), as well as domestic grazing animals and some exotic plants, were identified and subsequently removed or minimised. Hinewai is fenced off against stock but only limited predator management has been carried out (Wilson 2003). Reintroduction of species to Hinewai has been limited to 72 tūī (*Prosthemadera novaeseelandiae*), which were released in April 2009 and May 2010 (Banks Peninsula Conservation Trust 2010).

Hinewai Reserve was chosen as a case study site for this thesis as the management strategy has been consistent over the entire time frame, which is quite challenging to find in New Zealand. In addition, the mosaic of different successional stages over the reserve enables the application of a space-for-time substitution (chronosequence) covering a time frame between 87 to 120 years (see section 3.3.2 for more information).

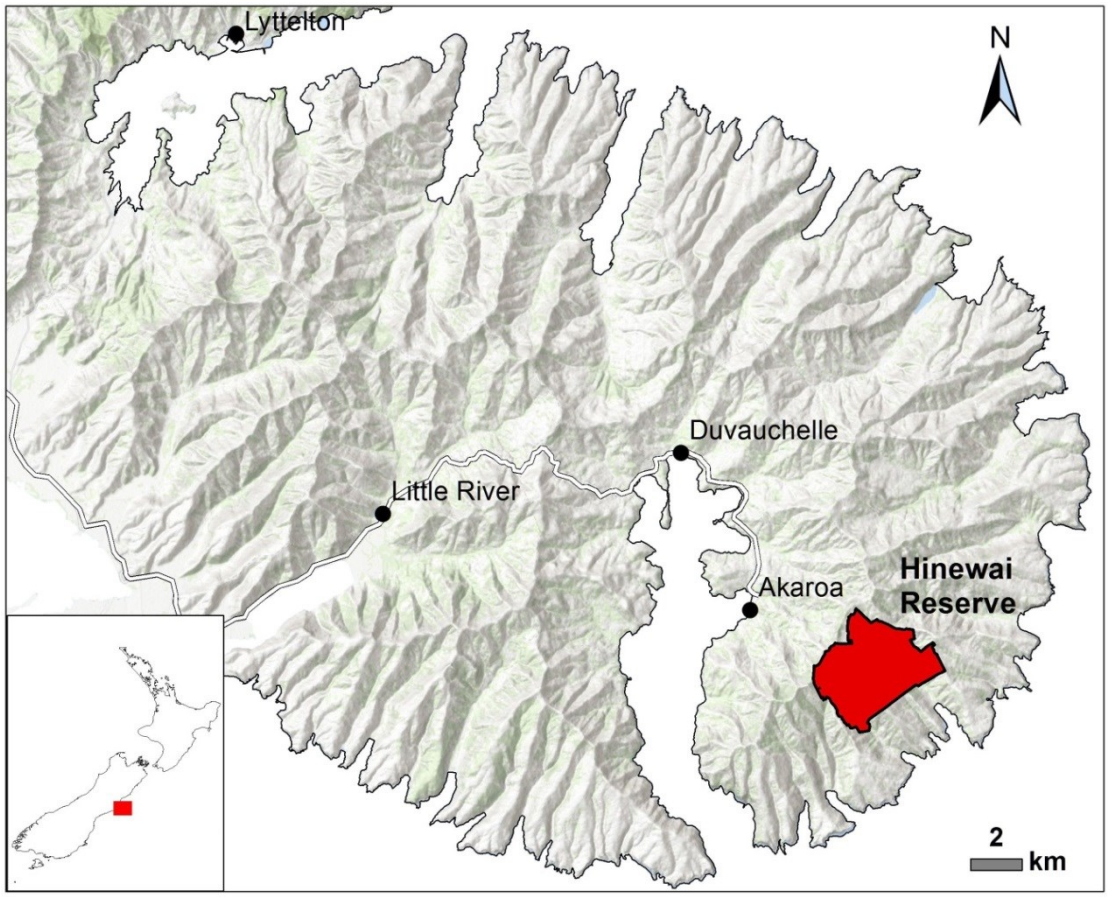


Figure 2. Map showing the location of the study area, Hinewai Reserve on Banks Peninsula on the east coast of New Zealand's South Island.

Chapter 2
A Framework for Selecting Forest Ecosystem Attributes for Biodiversity Offsets

2.1. *Abstract*

One of the greatest conceptual challenges associated with biodiversity offsets is the choice of ecosystem attributes for offset modelling, as it significantly influences model performance and the resulting offset ratio. This occurs because attribute selection is closely linked to evaluating restoration success in offset projects. Determining which attributes are the most appropriate ones is currently compromised by the lack of a theoretical framework. The aim of this thesis chapter is to aid in developing such a framework as well as providing an up-to-date discussion of potentially suitable attributes. The concept of ecological integrity is suggested as a broad framework for goal setting and evaluation of biodiversity condition in offsets, as it specifically investigates ecosystem condition, trends, and sustainability. Consequently, attributes should be selected from four key groups contributing to ecological integrity at a site: ecosystem composition, structure, function, and resilience. A literature review was undertaken to identify a set of attributes which seem most suitable for broad scale application in biodiversity offsets. Performance for commonly applied attributes to determine restoration success and biodiversity condition in forests is discussed and scored against a set of criteria. Finally, a potential set of key attributes for evaluating biodiversity offset projects is highlighted as well as areas requiring more research to further improve or develop new attributes.

2.2. *Introduction*

Land use pressure is globally increasing due to a rising demand for energy, infrastructure, and resources (Harvey & Pilgrim 2011; Rands et al. 2010). Thus, solutions have to be found to merge development actions, sustainable resource use, and biodiversity management. Tools which can effectively place an economic value on biodiversity are likely to be especially important in the context of ongoing development (Pearce & Moran 1994). One approach to secure biodiversity conservation and to ensure sustainable economic development is through the use of biodiversity offsets. Offsets aim to ensure a no net loss and preferably a net gain for biodiversity in the vicinity of the development impact

site (BBOP 2012). To achieve this objective, biodiversity offset models need some measure – preferably quantitative – of the biodiversity currently present at the impact site, the anticipated loss of values through the proposed project on this biodiversity, and the future development of the offset site under the proposed conservation management. This quantification is based on measured ecosystem components, called attributes, which are selected as being representative for the biodiversity at the site (BBOP 2009c). Attribute choice is of great importance as it significantly influences model performance and the resulting offset ratio (NZBOP 2012). To ensure that offsetting does result in genuine biodiversity gains, rather than omitting ecologically important species, interactions or communities, attribute choice has to be soundly based scientifically. Ecologists all over the world are currently challenged with the difficult task to choose the most appropriate attributes for biodiversity offsets. Currently, there is no theoretical framework to guide this.

In this chapter, a conceptual framework is crafted for ecosystem attribute selection in forests and an attempt is made to identify an objective, practicable, and defensible set of key attributes. The first part of this chapter explores the link between restoration and biodiversity offsets. This is followed by a discussion of the use of ecosystem integrity as a broad framework for attribute selection. Important underlying premises that attributes have to fulfil are summarized and forest measures commonly used to assess forest condition or recovery are discussed. Finally, recommendations for attribute selection are made, a set of key attributes is presented, and further research requirements are highlighted.

2.3. *Biodiversity Offsetting and Restoration Ecology*

There are two main categories of biodiversity offsets; averted risk and restoration offsets (Maron et al. 2012). Averted risk offsets place a protection status on sites that are not legally protected and are under threat of biodiversity loss. This type of offset is not discussed in this paper, which focuses on ecological restoration. Restoration offsets are most commonly form of offsets; they can be divided into enhancement and active restoration offsets. Enhancement offsets aim to improve native biodiversity condition at a degraded site that already has some native biodiversity values present; whereas active restoration offsets (re-) create ecosystems by replanting areas such as abandoned pasture. In a sense, most biodiversity offsets are restoration projects, and therefore for offsets the ultimate goal is to assess when the restoration has been successful.

Hence, the question of attribute choice is closely linked to defining the restoration goal and measuring restoration success.

The overall goal of biodiversity offsets is to achieve at least a no net loss of biodiversity by restoring native biodiversity at the offset site (BBOP 2013). Several issues derive from choosing restoration of such a complex and broad concept as biodiversity as the project goal, especially given confusion surrounding its definition (Kaennel 1998). Noss (1990) suggested focusing on the three key components describing ecosystems, composition, structure, and function, as the basis for goal setting. But is biodiversity truly the overall restoration goal? In biodiversity offsets we are not only interested in the inventory of a site (biodiversity) but also in its condition, trends, and sustainability. It seems that in order to restore biodiversity at a site we have to aim for an even more encompassing concept.

Ecosystem integrity has been suggested to provide a useful framework for assessing ecosystem condition and the effectiveness of management actions (Angermeier & Karr 1994). It has been defined as a measure of ecosystem condition, evaluating its composition, structure and function in relation to the system's natural or historical range of variation (Tierney et al. 2009). Integrity considers ecosystem condition over time, focusing in particular on the influence of anthropogenic disturbance and the stability or resilience of the ecosystem. Ecosystem integrity also includes the concept of 'native biodiversity' as an essential component (Angermeier & Karr 1994; Noss 2000). This makes integrity especially appealing for biodiversity offsets, as offsets are usually used when native biodiversity is impacted by a development project. The restoration goal will in most cases be to restore native ecosystems, with reference to historical conditions (BBOP 2009b) or simply to achieve high ecosystem integrity (i.e. to retain or enhance a high native component). Ecosystem integrity also requires the ecosystem to be self-sustaining in the long run and with that to possess a high level of resilience (De Leo & Levin 1997).

Combining Noss's (1990) approach with the concept of ecosystem integrity provides a useful framework for assessing restoration success by focusing on attributes in the following key groups: structure, composition, function, and resilience. This framework is very similar to Shackelford's et al. (2013) categories for attributes listed by the SER Primer (2004) for assessing restoration success. The only difference is that they considered landscape context as a separate category. This thesis follows Noss's (1990) biodiversity approach where structure,

composition, and function encompass different spatial scales including the landscape context as well as different levels of organisation. His approach is further extended here by also including resilience into the conceptual framework to identify a set of attributes for the assessment of restoration success.

2.4. *Evaluation Criteria for Attribute Selection*

The attributes sought for evaluating offsets are essentially ecological indicators, intended for unravelling condition and trends of forest integrity. There is a huge body of literature surrounding indicator selection, and the factors that make a good ecological attribute (indicator) for management, monitoring or impact assessment have been widely discussed (Andreasen et al. 2001; Heink & Kowarik 2010; Lee et al. 2005; Noss 1990). Most authors come to similar conclusions that attributes should be:

1. holding a high ecological information content, providing a good proxy for different aspects of the target ecosystem
2. easy to measure and cost-effective in terms of time, expert level, and equipment required
3. well researched, in terms of their response to changing ecosystem conditions, showing a predictable response to changes in ecosystem condition
4. feasible to analyse and interpret
5. relevant to restoration objectives, i.e. able to reflect condition and trends of structure, composition, function or resilience components at a site
6. sensitive to changes in ecosystem condition, showing change within the project timeframe and react to the management applied
7. not correlated with other attributes used
8. distinguishing between human induced and natural changes (e.g. natural succession)

Point eight is of special importance as offsets have to demonstrate that biodiversity gains occur because of management actions (additionality) (ICMM & IUCN 2012). It is a particularly difficult criterion to fulfil; ecosystems are naturally always in flux and constantly changing (De Leo & Levin 1997).

There is consensus within the literature that no attribute can fulfil all these requirements. This fact and the complexity of ecosystem integrity demand a carefully chosen set of indicators (Carignan & Villard 2002; Noss 1990).

For evaluating attribute efficacy for biodiversity offsets the criteria listed can be sorted into two broad groups. Criteria 1-4 refer to the inherent characteristics of attributes that can be assessed in general, reflecting overall suitability, and have been reviewed in the following sections to identify a key attribute set. The evaluation of the second group, criteria 5-8, largely depends on the specific project and is not discussed here.

2.5. *Which Ecosystem Attributes Exactly?*

It is reasoned within the restoration literature that no ecosystem attribute will be applicable in all situations and therefore attribute selection needs to be relevant to the specific project (e.g. Andreasen et al. 2001; Failing & Gregory 2003). While this might be partly true, there will be attributes that are almost generally applicable for assessing restoration success and are as a consequence commonly used in projects (see Ruiz-Jaén & Aide 2005a). I now review attributes describing the structure, composition, function, and resilience of an ecosystem that are relevant to restoring forest ecosystems. We concentrate on the more commonly applied or suggested attributes for assessing restoration success (Ruiz-Jaén & Aide 2005a) and ecosystem condition (Aronson et al. 1993a, 1993b; Parkes et al. 2003) or attributes recommended for biodiversity assessment (Oliver et al. 2007). Not all suggested attributes are discussed here as, for example, Aronson et al. (1993a, 1993b) focused on arid and semi-arid lands. The same applies to biological interactions that are often used for assessing restoration success (Ruiz-Jaén & Aide 2005a) but tend to be specific to individual projects.

2.5.1. Structure

For the purpose of this thesis, structure refers to spatial and temporal patterns of various habitat components.

Tree Diameter and Height

Tree diameter and height are easy to measure and a range of related measures can be derived from them. They relate well to productivity and ecosystem development. In addition, they also represent availability of key structures in forest (e.g. cavities, deadwood, habitat trees, and fuel load in fire-regulated

forests). However, very simplified measures such as the mean diameter do not distinguish well between successional stages (Franklin et al. 1981) due to a wider variation in diameter sizes in old forests (Bauhus et al. 2009). Attributes describing tree size diversity (TZD), such as the spread of diameters, have been suggested to perform better (Franklin et al. 1981). Simple measures of TZD such as the standard deviation of tree diameter at breast height (s_{dbh}) have been found to be highly correlated to more complex indices of stand structure (Neumann & Starlinger 2001). Other measures used include the frequency distribution of diameter. Still, its usefulness varied between studies (McElhinny et al. 2005) and their interpretation requires some subjective judgement (Lexerød & Eid 2006). Indices developed to investigate species richness or abundance have also been employed to evaluate tree size diversity (Lexerød & Eid 2006). Index choice depends on the forest ecosystem of question, with one of the most frequently used being the Shannon index (Valbuena et al. 2012). Though not frequently employed, the Gini coefficient was recommended for having only low sensitivity to sample size and being able to discriminate reliable between diameter distributions (Lexerød & Eid 2006; Valbuena et al. 2012). All the measures that can be used for describing diameter diversity could also be used for tree heights (Zenner & Hibbs 2000) or to develop combined measures. Overall canopy height is also often included into assessing restoration success (Ruiz-Jaén & Aide 2005a) and has been used as an indicator for successional stage (Castro-Luna et al. 2007).

Tree Density

Plant density is frequently measured in restoration projects (Ruiz-Jaén & Aide 2005a). The easiest but least precise measurement is the number of trees per hectare. More complex methods are available, integrating the variation within tree spacing and quantify spatial forest structure utilizing different indices; see McElhinny et al.(2005) for a short or Pommerening (2002, 2006) for a more detailed overview. As these methods require measuring inter-stem distances at the whole sampling plot in uneven-forests, they will not be discussed here any further. Tree density might not follow a predictable trajectory over time and the general usefulness of calculations of tree densities in offset projects is questionable, as more useful information can be gained by investigating shifts in diameter distributions or trends in basal area (Chazdon et al. 2007).

Stratification

Layering is a key element in forests, providing a wide range of biotic resources like food and nesting sites which generates a close relationship between the distribution of foliage and occurrence of birds, bats, insects, small mammals, and epiphytes (Grelle 2003; Moorhead et al. 2010; Pereira et al. 2010; Rodgers & Kitching 1998; Schulze et al. 2001). Because of its ecological importance forest stratification is commonly assessed in restoration projects, biodiversity offsets or for other biodiversity monitoring purposes (e.g. Morrison & Lindell 2011; Munro et al. 2011; Solid Energy New Zealand Limited 2009; Tripathi & Singh 2005; Wiser et al. 2001). A range of measures from very simple (species per height class/strata, cover % of different life forms/ages per tier) to very sophisticated (strata as light transmission segments) are available (Parker & Brown 2000). However, cover percentages of different life forms or species per strata seem to be the most feasible measures in terms of ease of measurement, but their suitability for assessing recovery of forest structure and with that restoration success needs to be tested.

Canopy Cover

Canopy cover is an indirect measure of canopy light absorption as it refers to the percentage cover of the vertical projection of tree crowns on the ground (Newton 2007). It is also a measure of tree dominance at a site (Jennings et al. 1999) and is a surrogate for land stability (Solid Energy New Zealand Limited 2009). Canopy cover is related to tree diameter, basal area, and stem density (Fiala et al. 2006). A range of methods are available for measuring canopy cover from simple cover scales (Hurst & Allen 2007) to the use of hemispherical photography (Gonsamo et al. 2013). Canopy cover can be an easy and rapid measure, but to achieve higher accuracy some of the more complicated methods need to be used, which become more labour intensive.

Measures of important Habitat Structures

The suitability of key features like habitat trees might be best investigated by the individual project. They are often linked to specific species of conservation interest. In addition, they can take a long time to develop and are therefore more appropriate for later successional forests. For coarse woody debris (CWD) similar issues arise but, even though the sought after larger dimension and diameter distributions will most likely establish in later successional stages, it is an ongoing process which could be easily monitored and indicate a steady increase

in habitat quality. CWD has occasionally been included in biodiversity offset projects or restoration success assessments (City of Bainbridge Island 2009; Majer et al. 2007).

Leaf Litter

Leaf litter plays a key role in decomposition and nutrient cycling, representing diversity and functional hot spots in forest ecosystems (Hansen 2000). Consequently, studies evaluating restoration success occasionally include a measure of leaf litter structure or volume such as cover percentage, number of litter layers or litter depth (Ruiz-Jaén & Aide 2005a). It has also been suggested as an indicator of disturbances and its potential importance for the recruitment of plant species has been emphasized (Parkes et al. 2003). However, dynamics between litter structural complexity, depth, litter invertebrate richness and composition are complex and results vary between studies (see Brennan et al. 2006; in comparison to Hansen 2000; Zeppelini et al. 2009).

2.5.2. Composition

This is the group of inherent attributes most closely linked to the traditional biodiversity concept and is often used synonymously for diversity (Ruiz-Jaén & Aide 2005a; van Andel et al. 2012). For the purpose of this thesis, composition encompasses all species related measures, providing information about their variety and abundance. To restore community structure, species composition and diversity at a site is a common restoration goal and is thought to be a key measure of restoration success (Society for Ecological Restoration International Science & Policy Working Group 2004).

Species Diversity Measures

The fundamental issue of diversity indices is that they suffer from complex species information being reduced to single numbers (Feest 2006; Purvis & Hector 2000; Rayfield et al. 2005). In addition, they are also highly dependent on sample size and effort (Gotelli & Colwell 2001, 2011). Another potential issue is that for all diversity measures organisms have to be reliably identified (Bacaro et al. 2009; Chiarucci et al. 2011). This fact may confine the species group chosen for a project, biasing it to the ones easiest to measure and not the ones with the highest information content. It is also often not realized that the data used to estimate diversity represent just a sample of the community and not its entirety. For a meaningful comparison between sites, biodiversity measures need to be

corrected (e.g. rarefied) to account for differences in samples sizes (Maurer & McGill 2011).

In the ecological literature, species richness is the most common measure of species diversity and usually takes the form of a species list (Purvis & Hector 2000; Stirling & Wilsey 2001). It is also the most applied diversity measure for assessing restoration success (Ruiz-Jaén & Aide 2005a). However, species diversity measures do not tell us much about the condition or change in species composition (Rayfield et al. 2005; Spellerberg 2005). Then again, they are generally easy to calculate and interpret and have a long history of application (Buckland et al. 2005; Lamb et al. 2009). Biodiversity measures (e.g. Simpson, Shannon diversity) might, however, be useful to compare the same sites in time or space, when holding the sampling procedure constant but need to be accompanied by other measures of composition to investigate causes of change (Mitchell 2005). Special care should be given to index choice. They vary in being more or less sensitive to sample size and also tend to give different weights to either common or rare species (Gotelli & Colwell 2011; Spellerberg 2005).

In addition to studying the number of species and their distribution, other ways exist to express the diversity of organisms. Some authors regard diversity indices as more useful when they focus on taxonomic relatedness or differences in functional traits (see Desrochers & Anand 2004). Taxonomic distance for different taxa is usually calculated by investigating the path length along a phylogenetic tree. It has been suggested that taxonomic diversity indices (Srivastava et al. 2012), especially taxonomic distinctness (sensu Dornelas et al. 2011), might be able to act as indicators for anthropogenic introduced stress in ecosystems. In recent years a strong link between ecosystem functions and phylogenetic diversity has emerged, hence it has been put forward as a good measure of ecosystem resilience (Cadotte et al. 2011). Phylogenetic diversity was also found to have the same predictive power for ecosystem function as functional diversity; it can be used even if the specific traits for the organisms are not known (Flynn et al. 2011; Montoya et al. 2012). However, phylogenetic diversity has been rarely used in a restoration context and, as far as the author is aware, only in fresh water ecosystems (e.g. Marchetti et al. 2010). In addition, it is difficult to quantify unless good phylogenetic information is available.

Species Composition

Methods commonly used to evaluate restoration success are classification, ordination, and similarity indices (Ruiz-Jaén & Aide 2005a). They can be used to identify trends in successional pathways at a site (e.g. Heiri et al. 2012) and to reveal underlying causes of community change (Jost et al. 2011). Unfortunately, compositional measures can also be sensitive to total or unequal sample size (Chao et al. 2006). Species abundance distributions (SAD), e.g. rank abundance plots have been employed to evaluate community change, especially in reaction to disturbance (e.g. Dornelas et al. 2011). Matthews and Thomas (2015) recently reviewed how SAD could be used to assess ecosystem integrity and the effect of management action. This promising tool should be further validated to enable its use in restoration settings. An emerging pattern in the literature is the recognition that ecosystem integrity could be most meaningfully evaluated by subsetting community data and using key ecological properties like dispersal mode (see resilience measures) (Funk et al. 2008; Matthews & Whittaker 2015). Compositional measures are valuable tools in unravelling trends and status of taxa and should be included as attributes, preferably examining different species groups and trophic levels (Ruiz-Jaén & Aide 2005a).

2.5.3. Forest Processes/Functions

The definition of function for the purpose of this thesis includes all ecosystem related abiotic processes and biological functions performed by different life forms and the interactions of these (Society for Ecological Restoration International Science & Policy Working Group 2004). Attributes from this group generally take longer to recover and are more resource intensive to measure than compositional and structural measures (Ruiz-Jaén & Aide 2005a; Wortley et al. 2013).

Nutrient Cycle

The status of soil nutrients (Fuhlendorf et al. 2002) and their ratios (Gomes & Luizão 2012), in addition to pH values and cation-exchange capacity (CEC) (Areola et al. 1982; Feldpausch et al. 2004; Langer et al. 1999), can indicate current soil fertility and health. The formation of soil organic matter (SOM) has been identified as a key attribute of soil development or health and has been recommended for inclusion in restoration success evaluations (Aronson et al. 1993b; Koch & Hobbs 2007). It is also an important measure of the plant available nutrient pool, which is highly susceptible to land use (Schlesinger

1984). Despite some criticism, the SOM C:N ratio is regarded as an indicator for N mineralisation and soil quality (Ostrowska & Porębska 2015; Piñeiro et al. 2006). Both nutrient pools as well as SOM measures are commonly applied to assess restoration success (Ruiz-Jaén & Aide 2005a).

Microbial biomass, composition, and activity in particular have been proposed as early indicators of soil ecological stress or management effects; they reflect soil biota activity (Haselwandter 1997; Six & Jastrow 2006) and possess a shorter reaction time to change than total organic C or N (An et al. 2013; J. A. Harris 2003). Microbial measures, such as microbial exoenzymes representing different producers, are occasionally included in assessing restoration success or management options (e.g. Arunachalam & Pandey 2003; Boerner et al. 2008). SOM turnover, especially that of the labile fraction, can also indicate soil biota activity and provides a more precise estimate of soil quality than SOM content (Haselwandter 1997; Six & Jastrow 2006).

Unfortunately, these microbial measures need further refinements before they can be more generally applied in assessing restoration success because of contradictory responses to management and/or a lack of standard analysis methods which makes results difficult to interpret (Gil-Sotres et al. 2005). Furthermore, while measures of microbial biomass are relatively easy, they are a black box approach that provides no information about the composition or activity of the microbial community (Schloter et al. 2003).

Leaf litter decomposition is also occasionally employed in restoration projects to evaluate nutrient cycling (e.g. Borders et al. 2006; Grant et al. 2007). Measures range from calculating the decomposition constant k by assessing leaf litter fall and mass of ground leaf litter (Ruiz-Jaén & Aide 2005b) to more complex measures of examining mass loss in leaf litter bags (Borders et al. 2006). Even though leaf litter decomposition rates relate to biotic activity, they are strongly influenced by site conditions and litter quality (Eijsackers & Zehnder 1990). Moreover, data collection for assessing leaf litter decomposition is time-consuming.

Therefore, soil nutrient status, pH values, CEC and SOM measures seem to be currently the most reliable and easiest ways to assess nutrient cycling for assessing biodiversity offset projects.

Energy Capture/Productivity

Vigorous vegetation growth has been suggested as a good indicator of restoration success, integrating all aspects of soil fertility and driving the recovery of other biological components such as microbial communities (Jasper 2007). Aboveground biomass accumulation can be estimated in various ways, for instance by investigating leaf litter fall and tree related standing biomass (Feldpausch et al. 2004; Rhoades et al. 1998). As a surrogate measure, tree basal area is sometimes used for assessing tree standing biomass (D. A. Wardle 2009). Both basal area as well as plant biomass are commonly assessed in restoration projects (Ruiz-Jaén & Aide 2005a). However, ecosystems can have high productivity during early stages of degradation due, for example, to rapid colonisation of weeds (Aronson et al. 1993b; Odum et al. 1979), and so biomass by itself provides limited information about forest integrity.

Regeneration (Recruitment)

Tree regeneration potential and success are key attributes in forest ecosystems as dispersal limitations can represent critical filters in restoration projects, impeding the establishment of species at a site (Battaglia et al. 2008). Natural regeneration potential can be identified by examining factors like seed rain, viable seeds in soil seed banks (Aronson et al. 1993a), distance to and number of seed trees (Holl et al. 2000; Ingle 2003), but its usefulness will largely depend on the individual project. It can also be more easily measured directly by sampling seedling and sapling density, which is more suitable for a broader scale application (Bailey & Covington 2002; Battaglia et al. 2008; Maza-Villalobos et al. 2011).

2.5.4. Resilience

Resilience is the ability of an ecosystem to maintain its composition, function, and structure in the face of the normal ranges of stress and disturbance (Drever et al. 2006; Society for Ecological Restoration International Science & Policy Working Group 2004).

Interestingly, even though the importance of ecological resilience for ecosystem restoration is widely recognised (Society for Ecological Restoration International Science & Policy Working Group 2004; Suding 2011), it is rarely included as a project goal (Hallett et al. 2013) and as consequence hardly ever assessed (Clewell & Aronson 2013). This might be rooted in the confusion over its

definition as well as its difficult valuation. Even though the notion ´resilience´ has recently received much attention in the literature (e.g. Angeler & Allen 2016; Hodgson et al. 2015; Standish et al. 2014; Suding 2011), the surrounding conceptual and methodical issues (i.e. how to quantify it) are far from being conclusively resolved.

Functional and Response Diversity

It has been advocated that species traits, and with that functional diversity, might be a good predictor of resilience (Elmqvist et al. 2003). Due to the fact, that functional group members are responsible for sustaining ecosystem functions (Peterson et al. 1998). This view is supported by the SER Primer (Society for Ecological Restoration International Science & Policy Working Group 2004), which states that one criterion for restoration success is the presence of all functional groups, important for long term ecosystem stability.

Indices like functional diversity have been emerging and can be divided into richness, evenness, and divergence (Schleuter et al. 2010). The assumption is that the more species are present in a functional group (fulfilling similar functional roles = functional effect groups), the higher is the probability that in case of a disturbance, species remain to take over important processes or functions (functional redundancy). It has also been suggested that this might not be the case if species react differently to stressors or disturbances (Laliberté et al. 2010). Species identity and the spectrum of stress tolerance in a group (response diversity) might therefore be more important than the mere number of species (Elmqvist et al. 2003).

Response diversity was also proposed to be correlated to ecosystem resilience and thus a good indicator of it (Chillo et al. 2011; Elmqvist et al. 2003; Mori et al. 2013; Suding & Hobbs 2009). However, it remains an area of ongoing research as the underlying mechanisms are still poorly understood and its indicator value has been hardly tested. Functional diversity measures are generally more labour intensive to assess than traditional diversity measures. It also remains challenging to assign species to functional groups or traits in restoration projects (Laliberté et al. 2010) for less well known taxonomical groups such as bryophytes (Hedberg et al. 2013) and invertebrates. In addition, the overall question remains: which functional traits are providing the best proxies for different aspects of ecosystem function and with that for resilience (Cadotte et al. 2011)? Some studies suggested that the trait of the dominant species could have a greater effect on some ecosystem processes then functional diversity measures

(Mokany et al. 2008). If this can be further validated, the identity and condition of the dominant species in a community may provide a good proxy for ecosystem function.

2.5.5. Landscape factors

Species persistence can be greatly affected by connectivity, size, and quality of habitats left within a landscape (Crooks 2002; Franken & Hik 2004; Honnay et al. 2005). Species loss might lead to a decrease in functional diversity which in turn is thought to result in reduced ecosystem resilience (Cumming 2011).

Even though landscape factors are known to have the potential to constrain success in restoration projects (Suding 2011), they are seldom assessed (Brudvig 2011; Ruiz-Jaén & Aide 2005a) but see Gould & Mackey (2015) for a recent example. Once beyond the stage of choosing the strategically best location for a project, measures related to focal patch characteristics will be in many cases of most interest to the individual restoration site. These metrics are nowadays usually easy to calculate and cost effective to apply (Fabien Quétier & Lavorel 2011; Saura et al. 2008). Two main questions are asked: how well is the patch connected to other ones (isolation), and how likely are populations to persist in the patch (patch geometry)?

Connectivity

Connectivity relates to how freely organisms can interact within a given landscape (dispersal limitations). The most commonly used and easiest to compute metrics are distance based measures assessing structural connectivity. They are usually nearest-neighbour measures such as distance to the nearest patch, or distance to the nearest habitat patch(es) occupied by certain species / habitat type of interest (Prugh 2009). These measures have been criticized as being over simplified, and especially 'the distance to the nearest patch' performed poorly as a proxy for actual connectivity (e.g. Moilanen & Nieminen 2002; Prugh 2009; Tischendorf et al. 2003). Prugh (2009) found that the next-simplest measure, distance to the nearest occupied habitat patch showed much better results as a predictor of colonization. Connectivity has also been assessed using buffer based measures such as number of patches or corridors within a certain radius surrounding the focal patch. Even though they have been criticized for being sensitive to the buffer radius chosen, simulation studies show that they generally are a good predictor of between patch immigration (Bender et al. 2003; Moilanen & Nieminen 2002; Tischendorf et al. 2003).

Patch Geometry

Patch size, quality, and shape are important determinants of a patch's suitability to sustain populations (Fahrig & Merriam 1994). Due to species minimum area requirements, smaller patches often possess only a subset of their typical community (Noss 1983), and thus functional diversity and resilience are likely to be reduced (Cumming 2011). Furthermore, the smaller a patch the more dominant becomes the edge effect; the influence of external factors (Noss 1983; D. A. Saunders et al. 1991) and the difference in environmental conditions (such as temperature, wind, light) between forest edges and their core area (Forman & Godron 1981; D. A. Saunders et al. 1991). It can be assessed using patch shape measures such as the perimeter-to-area ratio (for an overview see Saura et al. 2008). Patch shape complexity has also been found to be a measure of surrounding land-use intensity (Moser et al. 2002; Saura & Carballal 2004).

2.5.6. Stressors

Presence of stressors at different hierarchical levels, particularly as a result of historic management such as introduced species or soil disturbances, has been used to assess resilience status, and with that restoration success (Hallett et al. 2013), because they can have a severe effect on ecosystem function and biodiversity (Srivastava & Vellend 2005). The occurrence of barriers (stressor induced thresholds that the system cannot overcome by itself and may lead to a regime shift) has been suggested to affect resilience and should therefore be investigated in restoration projects (Chillo et al. 2011; Elmqvist et al. 2003; Standish et al. 2014; Suding 2011).

Direct measurement

Obviously, it would be best to measure stressors and disturbances directly, but it might be often not possible due to costs or difficulties in measurement. In many cases, it will be more feasible to observe surrogate measures specific to the perturbation of interest, i.e. browsing pressure on a specific plant for introduced herbivores.

Surrogate Measures of (anthropogenic induced) Ecosystem Stress

Some measures that can indicate status or shift in stress or disturbance level are listed below.

- Community structure

A shift in species traits to better adapted "fitter" species caused by the changed environmental conditions occurs. These may be evident by shifts such as in dominance of species (i.e. Simpson index) (Caro 2010; Rapport & Whitford 1999), in size spectra (size decreases), trophic structure (Caro 2010; Rapport & Whitford 1999) or plant dispersal strategies (Janzen 1990).

- Environmental factors

Changes in measures of soil chemistry and physics (see section on functional attributes).

- Confounding factors at the landscape level

Factors such as isolation/fragmentation (affects meta-population dynamics), surrounding land use, and patch size/shape have been used to assess large-scale dynamics (see paragraph above).

- Natural disturbance regimes

Magnitude, frequency, and duration of natural disturbance regimes, as changes can lead to a loss in resilience (Folke et al. 2004)

2.6. *The Key Ecosystem Attribute Set*

All of the attributes discussed above which held a broad potential for assessing restoration success were scored in terms of their information content, well known characteristics, ease of measurement, and reliability of interpretation (see Table 2 for evaluation criteria). That was done for plants as they are the easiest and most commonly assessed taxonomic group (Ruiz-Jaén & Aide 2005a). Categories received different weights reflecting their importance for attribute selection. We regarded information content to be of the highest importance for attribute selection, being the inherent reason for its measurement in the first place, and doubled its weight. The final score of each attribute should be treated as a guide only (Table 3). It provides an indication towards attributes that are likely to be most useful for assessing restoration success as part of biodiversity offsets. Criteria 5-8 can then be used to define a specific set of project attributes. Measures listed under the same subcategory (e.g. vertical stratification) are very likely to be correlated with each other (evaluation criteria 7). Hence, it might be better to use a subset of these. Attribute recommendations, suggested in other studies on attribute choice for restoration success assessment, are indicated in Table 3.

Measures listed with higher scores will be reliably applicable in many circumstances and for different forest types. However, higher scores are biased towards the more conservative and easier measures – a result of the research need surrounding the newer and more sophisticated attributes. If attributes like microbial activity or response diversity receive more testing in restoration settings, they possess high potential to gain importance for assessing restoration success in the future.

Table 2 Evaluation matrix used for assigning scores to ecosystem attributes.

Ease of measurement/data acquisition	**Weight**	**Rating**	**Score**
Measurement can be taken on the spot, one off measurement per time period (moderate training required)	1	3	3
- samples have to been taken from the field and processed somewhere else (e.g. lab), but processing is still relatively easy and inexpensive - specialist equipment has to be used in the field - additional information complementing the field data have to be gained (e.g. dispersal mode)	1	2	2
Processing of samples is expensive, time consuming or requires a specialist, no standardised sampling method available.	1	1	1
Feasible to analyse/ interpret			
Easy – straight forward, simple calculations	1	3	3
Medium – some issues such as using rarefaction methods for species richness, data transformations for similarity/dissimilarity indices.	1	2	2
Difficult – specialist analysis required e.g. modelling, multivariate analysis	1	1	1
Information content			
Works for different aspects of the ecosystem (proxy) or information cannot be gained by other measures. Is able to differentiate between successional stages or can detect changes in ecosystem condition.	2	3	6
Is one of many measures that can be used to assess the same ecosystem aspect, does not clearly distinguish between seral stages, or has a potential weak link to the ecosystem feature.	2	2	4
Low information content, it is not clear how this attribute relates to ecosystem integrity.	2	1	2
Well researched /known characteristics			
Attribute is well researched and has been used widely in the restoration literature.	1	3	3
Has been used occasionally.	1	2	2
Has rarely or never been used – characteristics not well known.	1	1	1

Table 3. All attributes discussed in this chapter are listed with individual criteria and total score. Fifteen being the highest possible score, representing attributes which seem most suitable for wider application in offset situations. Attributes which have been suggested by other authors (2-4) for ecosystem assessment or commonly used once in restoration projects (1) are indicated on the right hand side.

Ecosystem element		Attributes	Information content	Ease of measurement	Feasible to analyse	Known characteristics	Total Score	1. Restoration success, Ruiz-Jaén&Aide (2005)	2. Vital ecosystem attributes, Aronson et al. (1993a+b)	3. Vegetation condition, Parkes et al. (2003)	4. Biodiversity attributes Oliver et al. (2007)
Structure	Vertical Stratification	cover % of different life forms/species per tier	6	3	3	3	15	X	X	-	x
		species per height class/strata	4	3	3	3	13	-	-	X	-
		tree height diversity	6	3	3	1	13	-	-	-	-
	Tree related	canopy height	6	3	3	3	15	X	-	-	-
		canopy cover	6	3	3	3	15	X	-	X	-
		tree size diversity (diameter)	6	3	3	1	13	-	-	-	X
		woody debris (snags, logs)	4	3	3	2	12	-	-	X	-
		litter volume, cover	4	3	3	2	12	X	-	-	-
		tree density	2	3	2	3	10	X	-	-	-
		litter structure	4	1	3	2	10	X	-	X	X
Composition	Diversity	species diversity	4	3	2	3	12	X	X	-	-
		taxonomic diversity indices (phylogenetic diversity)	6	2	3	1	12	-	-	-	-
		species richness	2	3	2	3	10	X	X	-	X
	Composition	similarity indices/ordination techniques	6	2	2	3	13	X	-	-	-
		species abundance distributions	6	2	2	1	11	-	-	-	-
Function	Nutrient cycle	nutrient pools direct (chemistry)*1	6	2	3	3	14	X	X	-	-
		soil organic matter (total SOM stock or C:N)	6	2	3	3	14	X	X	-	-
		soil Microbial mass	6	2	3	2	13	-	X	-	-
		leaf litter decomposition	4	1	3	1	9	-	-	-	-
		microbial activity	6	1	1	1	9	-	-	-	-
	Energy Capture	standing biomass	4	3	3	3	13	X	X	-	-
	Regeneration	seedling, sapling density	6	3	3	3	15	X	-	X	X
Resilience	Functional groups	completeness of species pool	6	3	3	3	15	-	-	X	-
		functional diversity	6	2	2	2	12	X	X	-	-
		response diversity	6	2	2	1	11	-	-	-	-
	Stressors	shift in evenness/dominance	6	3	3	2	14	-	-	-	-
		shift in species traits (e.g. size spectra, dispersal mode)	6	2	3	2	13	-	-	-	-
	Patch connectivity	interpatch distances (e.g. nearest neighbour of the same habitat type)	6	3	3	2	14	-	-	-	X
		amount of habitat in a given radius around the focal patch	6	2	3	2	13	-	-	X	-
	Patch characteristics	patch size	6	3	3	2	14	-	-	X	X
		perimeter-to-area ratio (patch shape)	6	2	3	2	13	-	-	-	-

2.7. *Summary*

In forest ecosystems, measures for assessing restoration success are naturally centred on trees, especially focusing on structures that they supply for other organisms. Conveniently, plant structural attributes (e.g. tree diameter or height) seem to be the easiest and fastest to measure of all attributes. On the other hand, resilience, as well as some of the more meaningful compositional measures, seem to be more sophisticated and still are an area of ongoing research. However, even though it might be tempting, no restoration or offset project should be based on the assessment of structural attributes alone; they may disguise underlying issues. Oversimplification of ecological systems mirrored by a choice of not the most suitable, but the easiest ecosystem measure holds a high risk of project failure in the long run (Hilderbrand et al. 2005). Then again, Maron et al. (2012) cautioned that the use of difficult to define or measure aspects of the ecosystem increases the risk of failing in achieving restoration success. Therefore, it remains a thin line between choosing an easy to measure but almost meaningless attribute, and one that provides high information content but is difficult to measure, interpret, or predict, due to a lack of knowledge.

To add to this challenge, it seems clear from the literature review that there will be in most cases no quick and easy way to reliably assess ecosystem integrity and more sophisticated measures might be required (Maron et al. 2012). Alternatively, more work could be undertaken to link the easier to assess attributes, which mostly represent the 'black box' approach, back to more difficult features of the ecosystem. The crucial question is: what level of detail is required in attributes for assessing restoration success?

Especially for biodiversity offset situations, where there is serious concern that rapid biodiversity assessment is just providing an excuse to further destroy valuable ecosystems for development purposes (Benabou 2014; Maron et al. 2012; S. Walker et al. 2009); more research input on attribute improvement is urgently required. Many questions concerning attribute selection and application remain unanswered, and the identified suitability criteria could not be evaluated in a comprehensive manner. This derives mainly from the fact that published studies rigorously testing multiple well-defined attributes are still scarce. This chapter has highlighted a potential set of key attributes for evaluating biodiversity offset projects as well as some of the areas requiring more research to further improve or develop new attributes. Within the next four chapters, the

suitability of most of these attributes to assess restoration success will be further assessed using data from a restoration project.

Chapter 3
Using Vegetation Compositional Measures to Establish Successional Pathways and Assess Restoration Success

3.1. *Abstract*

In this chapter, the successional trajectories and their stages are determined for the research area. This is important, as the chronosequence approach used in subsequent chapters is based on it. The quality of the two major chronosequences established for the research area are tested and time was found to be a stronger driver of successional processes than any measured environmental variable.

Even though every attempt was made to establish a chronosequence of high quality, some limitations could not be avoided. The major ones are the short observation time frame in relation to the life-spans of the dominant species and the uncertainty surrounding the successional endpoints of both pathways. These shortcomings are common to many restoration projects. The approach should, however, still be valid even though an unknown number of successional stages are missed, as trends are analysed over the observation time frame and not extrapolated. The reference forest is used as a guide only, where species composition might ultimately differ to the second growth forests. Structural characteristics are often shared between old growth forests and can be more relied on. Restoration progress was estimated by comparing the successional forests against the reference sites using a range of techniques.

All second growth forests were distinctly dissimilar in their woody and fern species assemblages to the reference sites, even after more than 80 years of recovery. Late successional species over 5 cm dbh were still mostly absent. The kānuka forests already displayed some colonisation by late successional species, while the mixed-broadleaved forest did not. Tools that apply similarity measures such as ordinations and PERMANOVAs are very useful to unravel general trends. Even more useful is the inspection of specific species groups such as late successional trees. The presence of these species in different life stages can be used to predict future successional stages and possible endpoints, as well as to detect restoration issues.

3.2. *Introduction*

Restoration of characteristic species assemblages has been regarded as a fundamental aspect of successful restoration (Society for Ecological Restoration International Science & Policy Working Group 2004). Convergence to historical species composition in restoration sites is often assessed by comparison to reference forests (Brudvig 2011; Ruiz-Jaén & Aide 2005a). Unfortunately, recovery of vegetation composition attributes can either be slow or absent (Jones & Schmitz 2009; Lebrija-Trejos et al. 2010; Suganuma & Durigan 2015). They can be also highly variable within and between sites, depending on small scale environmental conditions, disturbance level, seed sources and dispersal limitations (Lebrija-Trejos et al. 2010).

In this chapter, they are used as suggested by Ruiz-Jaén & Aide (2005a) to unravel successional trends in the research area and to build the foundation for subsequent chapters. The focus of this thesis was to test a range of promising ecosystem attributes for their ability to describe restoration success in a predictive manner. No long-term data set with concurrent management over the project life was available for restoration projects in New Zealand. Therefore, a space-for-time substitution, also known as a chronosequence, was applied to investigate ecosystem attribute development over two main vegetation trajectories at Hinewai Reserve. This approach assumes that different sites follow the same successional pathway, time being the major difference between them. The chronosequence method was originally used to investigate successional pathways (e.g. Billings 1938; Cowles 1899), but was also applied to biodiversity (Addison et al. 2003) and restoration studies (e.g. Aide et al. 2000; Brady & Noske 2010; Gould 2012; Reay & Norton 1999). This approach has frequently been criticized and is only valid if time is the main difference between sites (e.g. Johnson & Miyanishi 2008; L. R. Walker et al. 2010). Several suggestions have been made on how to establish a good chronosequence and are discussed in section 3.3.2.

The objective of this chapter is to establish and test the successional pathways at Hinewai, to verify the chronosequence used in the next three chapters. To achieve this, the vegetation trajectories suggested by Wilson (1994) are investigated. In particular, this chapter tests if time is the largest difference across the sequences and not variations in site conditions. Then restoration success in terms of convergence to a reference system is examined.

This was done by comparing similarity of woody and fern assemblages over progressing successional stages to a reference forest, the last remaining red beech forest (*Fuscospora fusca*) in the research area. Colonisation success of late successional trees within the different successional stages was determined. The purpose was to establish the possible climax forest type for both trajectories as well as to evaluate if forests are already in transition into a later successional stage.

3.3. *Methods*

3.3.1. Study Site and Research Design

While Hinewai Reserve covers 1250 ha, this research was undertaken in the original (oldest) part of Hinewai (109 ha). Reasons for this choice include logistical constraints e.g. large areas of gorse (*Ulex europaeus)* elsewhere at Hinewai), different times of purchase of the various land titles that comprise the reserve, and diverse environmental conditions. Due to wide variation in elevation, slope, aspect, topography, disturbance regime, and proximity to seed sources, many different vegetation trajectories are possible within Hinewai (Wilson 1994). To keep the number of possible ecosystem trajectories manageable, sampling plots were established on a similar aspect at an altitudinal range of 300 - 550m. Plant composition and its recovery speed change significantly outside of this environmental spectrum due to differences in rainfall (Wilson 1994).

The research area is still a patchy mosaic of different successional stages from pasture back to forest. Therefore, a stratified random sampling design was chosen. Successional pathways of the different patches as well as disturbance regimes were identified using aerial photos of the research area from 1941, 1964, 1984 and 2011. Stratification was then undertaken using the 2011 aerial photograph in combination with Hugh Wilson's (reserve manager 1987 to present) vegetation map from 1987, assigning areas to the estimated present vegetation type (Table 4).

ArcMap (ESRI 2011) was used to create random points within the different vegetation types, keeping a minimum distance of 30m from the edge. This relatively low edge distance was inevitable, due to a high spatial patchiness of vegetation in Hinewai.

In total 105 sampling plots were established using a handheld GPS device between November 2011 and January 2012 in Hinewai (Table 4, Figure 3). In addition, 20 plots were set up in directly adjacent farmland north of the Reserve. This area accommodates a similar successional mosaic to Hinewai, the only difference being the extensive grazing regime so it is representative of the pre-restoration state. Even though these additional plots are not analysed in this chapter, they are used in subsequent chapters and are mentioned here for completeness.

In each sampling plot, several terrain characteristics were recorded including physiography, altitude, aspect, and slope. Concentric plots were used to sample vegetation. Three vegetation tiers were inspected: fern, shrub, and tree. In both the shrub and tree tier, all woody species present in that layer were recorded. The shrub tier was defined as 0 - 3.5 m height and everything above was assigned to the tree tier. For the ground layer only fern species were recorded due to the virtual absence of herbaceous plants.

The fern layer was sampled within a 2 m radius circular plot and cover percentages for all species were recorded. All woody species ≥1 cm dbh (dbh=diameter at breast height, 1.40 m) were counted within a 6 m radius plot and affiliation with the tree or shrub tier was noted. In the same plot, cover abundances (%) were estimated for all woody species under 3.5 m height. This was necessary to account for shrub species, whose multi-leaders are generally difficult to count meaningfully. Hence, shrubs are better described by cover abundances. To account for the detection probability of larger tree sizes, especially in the old growth forest, all tree species ≥ 20 cm dbh were recorded within a 12 m circular plot. The 6 m (dbh > 5cm) and 12 m plot data were then combined to create the tree tier data set. Trees between 1 and 5 cm dbh were regarded to be saplings. Seedlings were sampled in four subplots of 1 m radius established 6 m East, South, West, and North of the main plot centre. Within the seedling plot all tree species < 140 cm height were identified and counted. Mean values across these four subplots were used for the analysis.

Table 4. Number of sampling plots established in each vegetation group / chronosequence in Hinewai. Approximate age range (years since establishment) of vegetation successional stages (vegetation group) based on historical aerial photos are also listed.

Trajectory	Vegetation group	Age span	No. of sampling plots	
			Hinewai	Control
Mixed-Broadleaved	Pasture	ca. 15	5	-
	Gorse	15-32	11	-
	Emergent natives	24-45	10	-
	Māhoe	38-70	12	1
	Fuchsia	42-87	16	6
Kānuka	Early	20-54	13	-
	Intermediate	80-105	9	10
	Late	100-120	11	-
	Old growth	>100	17	5
	Total		**105**	**22**

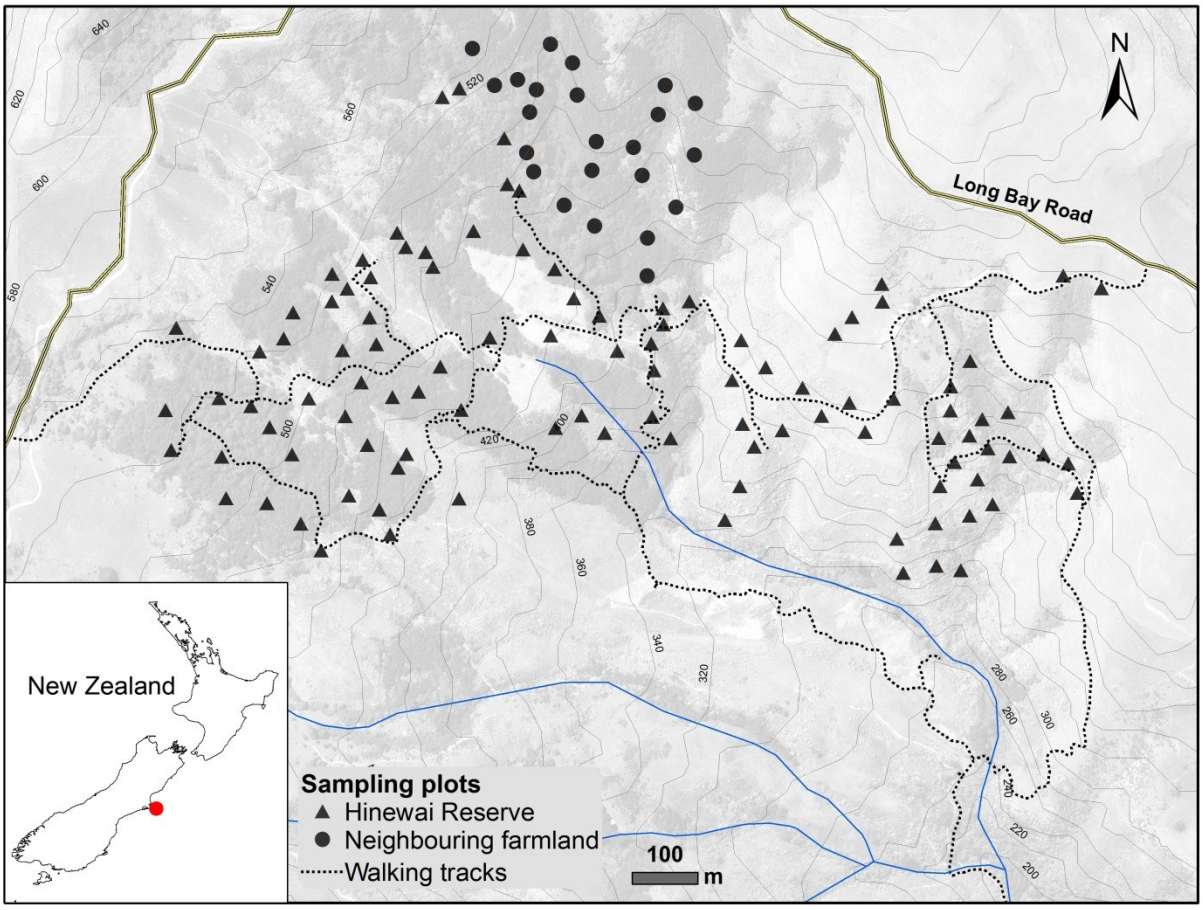


Figure 3. Map of the research area showing sampling plots located in Hinewai Reserve and the adjacent farmland.

3.3.2. Establishing the Chronosequences

Possible vegetation trajectories and their stages for the research area have been described by Wilson (1994) and were built on in this study (sensu Table 5). Allocations to these groups were based on vegetation structure and composition. Two main trajectories were investigated, the mixed-broadleaved and the kānuka (*Kunzea robusta*) trajectory. Individual successional stage description was updated according to results from the cluster analysis (see section 3.5.1). The kānuka sequence was divided into three stages (early, intermediate, late), reflecting its life cycle. Kānuka is able to establish in a range of habitats, including grazed pasture, gorse, and recently burned second growth (observations from aerial pictures sequence). It was not always possible to determine the exact starting point of the succession; however, pastures examined in this study were ungrazed and kānuka has been suggested to be unable to establish in ungrazed pasture (Allen et al. 1992; Esler 1978; Wilson 1994). Kānuka development was therefore observed in this study once kānuka has been established, forming a dense canopy.

The following phases were sampled in accordance to Wilson (1994), and other studies and are described in more detail in section 3.5.1: (i) early kānuka: kānuka establishes in either grazed pasture, gorse or burned mixed-broadleaved forest forming a dense canopy, (ii) intermediate kānuka: kānuka crowns begin to open up, facilitating the establishment of a dense layer of broadleaved species underneath. Finally, (iii) late kānuka: kānuka reaches its age limit of 80 to 150 years and subsequently dies off, thus promoting the increasing dominance of the broadleaved species (Allen et al. 1992; Burrows 1973; Smale et al. 1995). The mixed-broadleaved trajectory starts from (i) pasture, followed by (ii) gorse shrub, which is succeeded by the (iii) emergent natives, a transition phase where broadleaved species establish under gorse and finally, (iv) the mixed-broadleaved forest once the broadleaved species are shading the gorse, which subsequently dies off (Sullivan et al. 2007). Even though kānuka technically belongs to the broadleaved species, for the purpose of this thesis, the notion broadleaved species refers to species such as māhoe (*Melicytus ramiflorus*), fuchsia (*Fuchsia excorticata*), five-finger (*Pseudopanax arboreus*), mountain-five-finger (*Pseudopanax colensoi*), and others listed under the two mixed-broadleaved forest types in Appendix 1.

For the altitude sampled in this study, Wilson (1994) suggested kānuka forest would develop into a red beech (*F. fusca*) dominated forest. Whereas the mixed-

broadleaved forest might first be succeeded by a podocarp - broadleaved forest which eventually will also advance into beech (Wilson 1988). As a reference forest to assess how far succession had already progressed, only mature red beech forest was available within the study site. The recommendation given by Walker et al. (2010) on which criteria a chronosequence should fulfil was carefully checked (Table 6). Only one assumption could not be met; the two chronosequences did not cover the entire life span of neither the broadleaved nor the late successional species (*F. fusca* and *Podocarpus laetus).* Therefore, several successional stages as well as the ultimate climax forest types remain unknown.

Table 5. Two of many possible successional trajectories for the entire Hinewai Reserve as suggested by Wilson (Wilson 1988, 1994). (A) denotes the broadleaved and (B) the kānuka trajectory. This classification was used to stratify the research area. The only difference was an additional 'emergent natives group' between gorse and the mixed-broadleaved forest.

	Successional Trajectories					
	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Stage 6
	Age	0-15	>15	>40	>50	??
A	Pasture (500m)	Gorse	Mixed broadleaved forest	Mixed broadleaved forest	Podocarp - broadleaved forest	Fuscospora fusca forest
B	Pasture (500m)	Kānuka shrub	Kānuka forest	Late kānuka forest	Fuscospora fusca forest	Fuscospora fusca forest

Table 6. Requirements that an appropriate chronosequence should meet and their accomplishment in this study, following the recommendations made by Walker et al. (2010).

Important elements of a chronosequence	Hinewai Reserve	comments
Two or more stages (duration of time series depends on parameter of interest)	yes	at least 3 stages
Multiple stand characteristics that vary across stages	yes	
At least one independent verification of time series	yes	Aerial picture: 1941, 1964, 1984, 2011
Replication within stages	yes	
Sampling intervals within life span of every dominant species of interest or duration of process of interest	no	70 to120 years, but not the 900+ years which are required for the late successional species such as *P. laetus* (Ogden 1978; Wells 1972).
Multiple visits to study plots	yes	
Sere-appropriate measurements	yes	
Standardized measurements	yes	

3.4. *Analysis*

Testing the Chronosequences

To accommodate that the successional sequence encompassed shrub and tree dominated vegetation stages, species importance values were used rather than raw data. This relativization allowed using measures that better reflect dominance in different life modes. Depending on if the respective successional stage was tree or shrub dominated, tree counts and basal area calculations or shrub cover abundances were used. Species importance values (IV) for trees > 5 cm dbh were calculated using the following formula for forests (Bannister & Donoso 2013; Pascarella et al. 2000):

$$IV_{tree} = \left(\left(\frac{D_{sp}}{D_{tot}} * 100\right) + \left(\frac{G_{sp}}{G_{tot}} * 100\right)\right)/2$$

Dsp = species density per plot and D_{tot} = total plot density,
Gsp = species basal area within a plot and G_{tot} = total basal area per plot

For the shrub dominated stages (gorse and emergent natives) species cover abundances (%) were relativized to total cover observed per plot, as cover represents a dominance measure.

During fieldwork, it became apparent that there might be several distinct types of broadleaved forest in the research area. It was further uncertain if the transition phase 'emergent natives' was floristicly distinct enough to form its own successional stage. Hierarchical cluster analysis using the importance values for woody species was applied to check these grouping issues. The analysis was carried out on a Bray-Curtis dissimilarity matrix using the agglomeration method with the average linkage option (function 'hclust', package stats). The cophenetic correlation plot was examined to assess overall fit. Compositional pattern of vegetation groups were then graphed by using Nonmetric Multidimensional Scaling (NMDS) ordinations (function 'metaMDS', package vegan). Constancy tables for each group were calculated using package 'vegclust' (De Cáceres et al. 2010) to identify the dominant species.

Change over Time

At first, equal multivariate variance across groups was established (function 'betadisper', package 'vegan'). Then a Permutational Multivariate Analysis of Variance Using Distance Matrices (PERMANOVA) type 2 was deployed to test if time was the strongest predictor of compositional change rather than varying site conditions. Thus, it was a further test if all chronosequence assumptions

were fulfilled. Only compositional change over time could be assessed because vegetation groups were gained/checked by clustering (effect of vegetation groups on composition could not be statistically tested).

Similarity to the reference forest

Mean similarity for woody plants (species importance scores) and ferns between successional stages and reference sites were calculated using the Bray-Curtis distance and function 'meandist' (package vegan). The mean and its standard error for regeneration density per hectare (seedlings and saplings) of late successional tree species were calculated to assess progress towards the reference.

All analyses were done in R 3.3.1. (R Core Team 2016).

3.5. *Results*

3.5.1. Verifying the Successional Trajectories

Seven distinct groups were apparent from the cluster analysis on species importance values (Figure 4). One of these groups was only occupied by a single sampling plot (No. 49). Further investigation revealed that this particular plot experienced quite a different management to all others (pers. comm. Hugh Wilson). Kānuka trees were harvested in the mid-80s and young red beech trees were intentionally released. Consequently, this plot was removed from further analysis. Clustering within the ordination plots largely confirmed the predefined vegetation types, further supporting that the broadleaved forest consisted in fact of two distinct groups (Figure 5 and 6). It also supported the retention of the 'emergent natives' stage. Constancy tables revealed that dissimilarities between the two suggested broadleaved forest types were mainly due to the prevailing tree species being either māhoe (*M. ramiflorus*) (A) or fuchsia (*F. excorticata*) (B) (Appendix 1). Both groups showed minimal overlap on the broadleaved trajectory ordination plot (Figure 6). The three successional stages within the kānuka forest were not well separated in the dendrogram (Figure 4). In particular, young and intermediate kānuka were quite similar. This is mostly due to the patchy nature of the vegetation at Hinewai Reserve, rendering it impossible to avoid edge effects for some vegetation types. The younger kānuka plots (e.g. No. 48), classified closer to some intermediate plots, as they had some gorse and māhoe in the plot area, whereas the intermediate plots in this cluster (e.g. No. 83) had less broadleaved basal area in comparison to the other group members.

Still, the NMDS plot depicted the groups being compositional distinct enough to be meaningful (Figure 5). After re-inspecting the plot data, the decision was made, based on the vegetation definition given below, to maintain the plot classification. The stages used along the two main trajectories are shown in Table 7. Taking the results of the cluster analysis and the ordination plots into account, the final vegetation classification outlined below was used for this thesis. Successional stages (vegetation groups) are given in ascending order along the two main trajectories for the study area.

Table 7. Final selection of trajectories used throughout the remainder of this study. Mixed broadleaved forest trajectory types: A = fuchsia and type B = māhoe dominated. C denotes the kānuka sequence. The kānuka trajectory started in this thesis from the early kānuka forest, omitting pasture, as only ungrazed pasture was sampled in this study. Stages 5 and 6 are based on suggestions made by Wilson (1988, 1994) and only red beech forest could be sampled.

	Successional Trajectories					
	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Stage 6
A	Pasture	Gorse	Emergent natives	Mixed–broadleaved forest type A	Podocarp-broadleaved forest	*Fuscospora fusca* forest
B	Pasture	Gorse	Emergent natives	Mixed – broadleaved forest type B	Podocarp-broadleaved forest	*Fuscospora fusca* forest
C	Pasture/ Gorse/ burned mixed-broadleaved forest	Early kānuka forest	Intermediate kānuka forest	Late kānuka forest	*Fuscospora fusca* forest	*Fuscospora fusca* forest

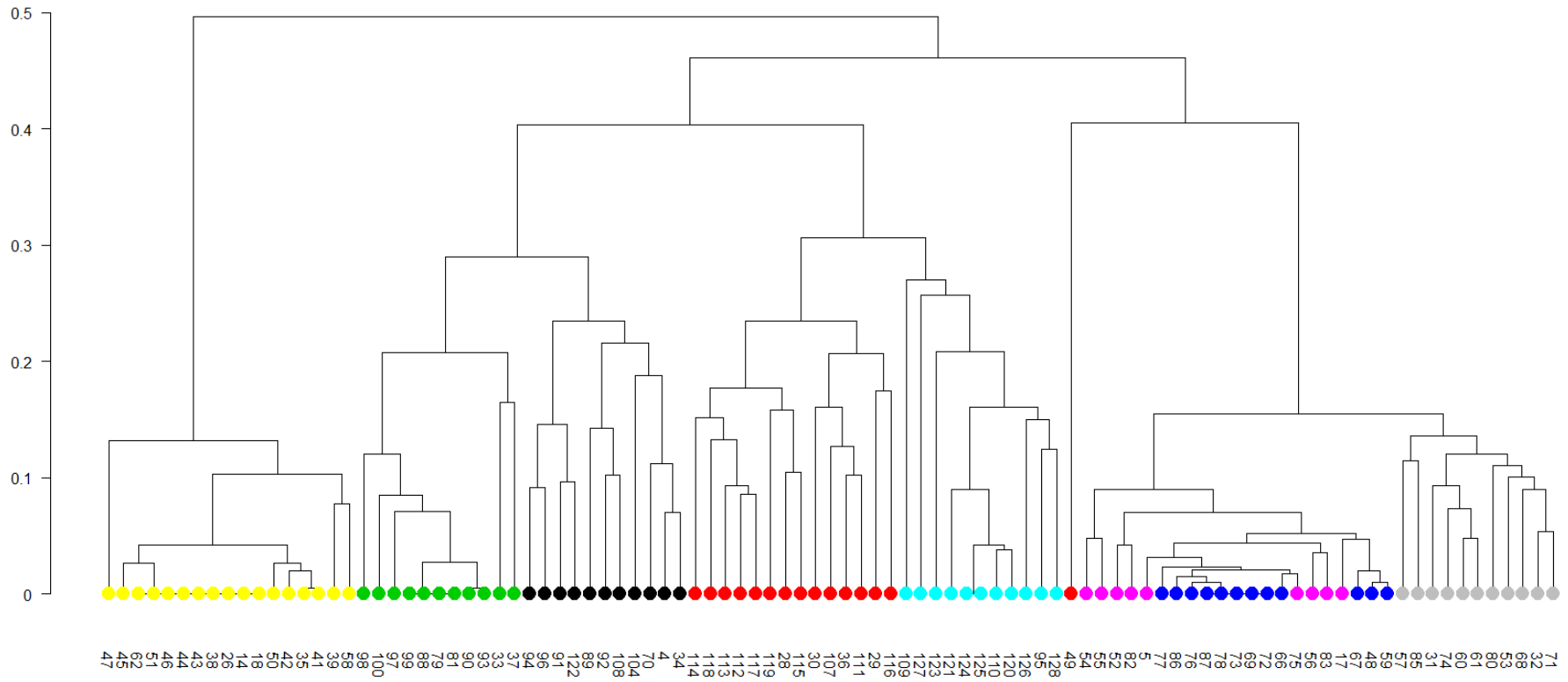


Figure 4. Cluster dendrogram showing the final vegetation class allocation for all plots. Sampling plot numbers are plotted vs the clustering result based on the species importance value data set (Hclust, Bray-Curtis). The 'mixed-broadleaved forest' class (red, light blue) has been split into two groups, one dominated by fuchsia (red) and the other one by māhoe (light blue). The kānuka group was not well separated according to their age (young=blue, pink=intermediate, old=grey), probably due to the 'Importance value' calculation, basal area of kānuka might be in both age classes similar (younger-more but thinner stems, intermediate stands=few, larger sized stems). Membership to the 'Emergent Natives' class (black) and 'Gorse' (green) was adjusted according to clustering results. Yellow plots depict the old growth forest.

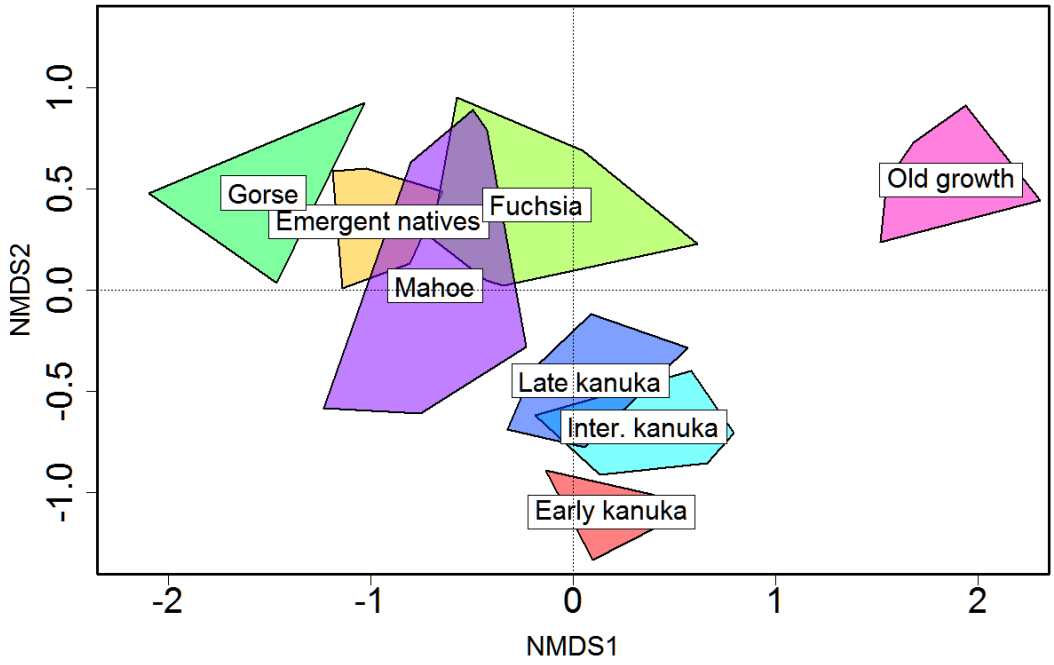


Figure 5. NMDS ordination plot using the Bray-Curtis dissimilarity (stress: 0.12, convergent solution, Wisconsin double standardization, perm=100) to further verify the distinctness of vegetation groups (species importance value data set) and to investigate successional pathways and similarity to the reference forest (=old growth).

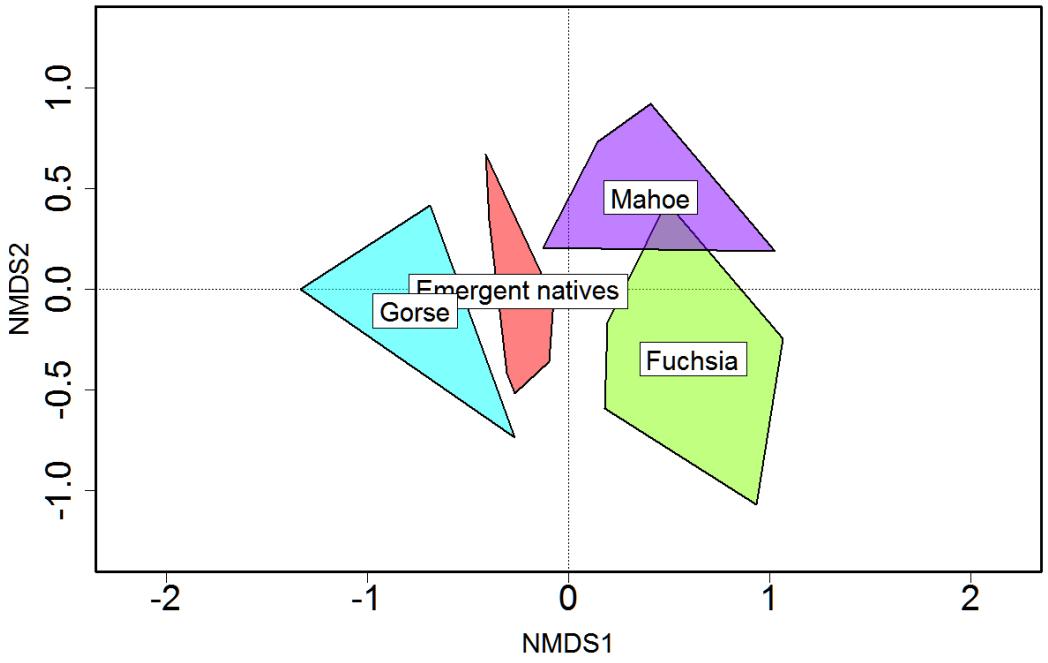


Figure 6. NMDS ordination on the species importance value data set for the mixed-broadleaved trajectory (Bray-Curtis dissimilarity, stress: 0.18, convergent solution reached, Wisconsin double standardization, perm=100).

(i) Mixed-broadleaved forest

Pasture

There are still some pastures left in the research area. Even though they have not been subject to grazing, frequent mowing maintained them as meadows in the past.

Gorse

Gorse (*Ulex europaeus*) is an exotic pioneer species, which establishes into pasture and can be the dominant species for up to 40 years in the absence of disturbances such as fire. Gorse as a nitrogen-fixer has the ability to improve soil fertility and is therefore regarded by some authors to be a good nurse plant (Lee et al. 1986; Wilson 1990). Sampling plots included in this category, are dominated by gorse (cover > 70 %), with only sporadic native trees/shrubs present.

Emergent natives

This transition stage from gorse to second growth mixed broadleaved forest is defined as having less than 70 % gorse cover and holds a moderate percentage of light demanding broadleaved species, especially māhoe (*Melicytus ramiflorus*), fuchsia (*Fuchsia excorticata*) and wineberry (*Aristotelia serrata*). These species will eventually overtop and shade gorse, which will subsequently vanish, as it is incapable of regenerating under its own shade.

Second growth-mixed-broadleaved forest

This diverse forest type follows the emergent natives successional stage, in some cases, especially along gullies it might also directly establish. Some typical species in varying densities include wineberry (*A. serrata*), seven-finger (*Schefflera digitata*), five-finger (*P. arboreus*) and mountain five-finger (*P. colensoi*). Dominant species are in most cases either fuchsia (*F. excorticata*) or māhoe (*M. ramiflorus*), therefore this forest was split into two subtypes. Wilson (Wilson 1988, 1994) suggested that this forest type will first develop into podocarp-broadleaved forest and then into red beech forest.

Subtype: Fuchsia-dominated mixed-broadleaved forest (A)

This type seems to be more frequent in moister areas of the research areas (e.g. gullies). The trajectory of this forest is unclear, but during sampling, it appeared that podocarp stumps were more frequent in this forest type than in the other. If this is a result of a higher past abundance of podocarps or by a difference in

management (e.g. gullies might not burn that well or podocarps left for shade) is not known.

Subtype: Māhoe-dominated mixed-broadleaved forest (B)
This forest is dominated by māhoe.

(ii) Kānuka forest

Early kānuka forest

This stage is characterised by kānuka (*K. ericoides sl.*) a native pioneer species which is able to colonise pasture. Kānuka and gorse often establish simultaneously in pastures, with kānuka outcompeting gorse after a few years (Wilson 1990). Aerial pictures also indicated its establishment into burned second growth forest. Sampling plots were classified as young kānuka, if the importance value for kānuka was greater than 85 and stand age was <30 years. These are very dense-single species stands, with other species very rarely present. Kānuka canopy height has not reached its maximum (<12 m).

Intermediate kānuka forest

Kānuka is still the dominant species, but kānuka canopy height has reached its maximum in the research area (ca. 12m). Kānuka crowns are becoming more open as result canopy cover is slowly decreasing, and other broadleaved species begin to establish (e.g. five-finger, mountain five-finger, and māhoe).

Late kānuka forest

These are older stands, kānuka is already in the process of collapsing, canopy cover is low, and a second tier of broadleaved species (mountain five-finger, five-finger, Māhoe) is well-represented and waiting to form the next canopy.

(iii) Reference forest

Red beech forest

This vegetation type is characterised by mature red beech (*F. fusca)* – with an unknown age with scattered podocarps such as thin-barked tōtara (*Podocarpus laetus*) present. These remnants have been altered by past management, such as logging, fire, and grazing. The sub-canopy layer is highly variable, depending on canopy openness. According to Wilson (1994) this forest represents the climax forest for the research area (300-550 m) and was therefore used as 'reference ecosystem'.

Podocarp-broadleaved forest

Unfortunately, this forest type is not present in the research area.

3.5.2. Verifying the Chronosequences

An assumption of the chronosequence approach is that age is the primary difference between sites and not environmental conditions (Johnson & Miyanishi 2008). PERMANOVA results indicated that time was indeed having the strongest effect on assemblages along all trajectories (Table 8 and 9). However, the effect size was rather low explaining just 18 % (kānuka) and 15 % (both broadleaved forests) of the overall differences in assemblage structure. All other effects were much smaller and no others were statistically significant.

Table 8. PERMANOVA type II results for the kānuka trajectory (without the reference forest), investigating effects of environmental variables and recovery time on woody plant composition using species importance scores (Bray-Curtis distance, perm = 999).

	SS	MS	Df	F	R^2	P
Time	0.166	0.166	1	6.7	17.6	**0.002**
Easting	0.027	0.027	1	1.11	2.9	0.323
Northing	0.026	0.026	1	1.03	2.8	0.358
Altitude	0.026	0.026	1	1.07	2.8	0.349
Physiography	0.035	0.017	2	0.7	3.7	0.618
Slope	0.009	0.009	1	0.37	1	0.771
Aspect	0.074	0.025	3	0.99	7.8	0.414
Residuals	0.546	0.025	22			
Total	0.943		32			

Table 9. Effect of environmental variables and recovery time on woody plant composition in the two mixed-broadleaved sequences; the reference forest was excluded. Depicted are PERMANOVA type II results (Bray-Curtis distance, perm = 999).

	Māhoe						Fuchsia					
	SS	MS	Df	F	R^2	P	SS	MS	Df	F	R^2	P
Time	1.104	1.104	1	10	15	**0.001**	1.227	1.227	1	9	15	**0.001**
Easting	0.060	0.060	1	1	1	0.625	0.335	0.335	1	3	4	0.073
Northing	0.104	0.104	1	1	1	0.387	0.152	0.152	1	1	2	0.298
Altitude	0.183	0.182	1	2	3	0.162	0.212	0.212	1	2	3	0.178
Physiography	0.367	0.183	2	2	5	0.137	0.630	0.210	3	2	8	0.107
Slope	0.066	0.066	1	1	1	0.603	0.072	0.072	1	1	1	0.672
Aspect	0.301	0.100	3	1	4	0.476	0.467	0.156	3	1	6	0.329
Residuals	2.350	0.107	22				3.283	0.131	25			
Total	7.267		32				8.225		36			

3.5.3. Compositional Similarity to the Reference System

Wilson (1988) predicted that all forests in this study altitudinal range will ultimately be dominated by red beech (*F. fusca*). He (1994) estimated that areas already holding mixed-broadleaved forest in 1987 will have been advanced into a podocarp-broadleaved forest by 2050, whereas the late kānuka forest will develop into a forest dominated by red beech. However, 18 years later both forest types are still dissimilar to the reference forest. Woody plant composition in the kānuka forest did not show measurable convergence to the red beech forest, as predicted by Wilson (Table 10). In fact, the NMDS plot suggests that kānuka is getting more similar to the broadleaved forests than to the red beech forest over time. This is a result of the dense layer of mixed-broadleaved species developing under the senescing kānuka. The major difference between the three second growth forests and the reference is mostly the absence of late successional tree species larger than 5 cm dbh, namely podocarps and beech trees (Table 11).

Table 10. Compositional dissimilarity of woody plants and ferns between vegetation groups from the two main trajectories compared to the reference forest. The two alternative stages for the broadleaved trajectory (māhoe and fuchsia dominated forest) are both displayed. Bray-Curtis dissimilarities on species importance values were used for calculation.

Trajectory	Stage	Woody plants	Ferns
Broadleaved	Gorse	0.99	0.98
	Em. Natives	0.99	0.97
	Māhoe	0.99	0.94
	Fuchsia	0.98	0.92
Kānuka	Early	0.99	0.92
	Intermediate	0.99	0.87
	Late	0.97	0.86

Podocarp saplings (mainly thin-barked tōtara) reached 21 % and red beech saplings 64 % of the reference forest in the kānuka forest. However, red beech regeneration was rather low with a mean of 42 saplings per hectare for the reference site. Interestingly podocarp seedlings and saplings were much more abundant throughout the reference site (mean/se= 645 ± 247). A reversed pattern was observed for the established trees, with an average of 10 podocarps and 96 beech trees per ha ≥ 5 cm dbh. No podocarps or beech saplings were observed under the mixed-broadleaved forests. Seedlings were only found in low numbers (under 5 % of the reference). Successional stages associated with the mixed-

broadleaved forests were on average further away from the reference forest than the kānuka groups (Table 12) and might therefore have a colonisation disadvantage. Another important aspect of the vegetation characterising the ground layer - ferns - also does not show a great similarity to the reference sites.

Table 11. Presence of late successional tree species in different size classes. Podocarps refer to *P. laetus* and *Prumnopitys taxifolia* for the regeneration and only to *P. laetus* for trees (> 5 cm dbh).

	Successional Stage	*Podocarps*						*Fuscospora fusca*					
		Seedlings		Sapling		Trees >5cm dbh		Seedlings		Sapling		Trees >5cm dbh	
		mean±se	*%*	*mean±se*	*%*	*mean±se*	*%*	*mean±se*	*%*	*mean±se*	*%*	*mean±se*	*%*
Broadleaved	Gorse	0±0	0	0	0	0±0	0	0±0	0	0±0	0	0±0	0
	Em. Natives	61±61	3	0	0	0±0	0	0±0	0	0±0	0	0±0	0
	Mahoe	0±0	0	0	0	0±0	0	0±0	0	0±0	0	0±0	0
	Fuchsia	0±0	0	0	0	3±2	30	50±50	1	0±0	0	3±2	3
Kānuka	Early	0±0	0	29±29	5	2±1	20	398±155	5	0±0	0	3±3	3
	Inter.	442±193	24	79±52	12	0±0	0	177±117	2	39±39	93	6±4	6
	Late	61±61	3	136±64	21	5±3	50	61±61	1	27±27	64	10±5	10
	Old growth	1826±378		645±247		10±5		8612±1932		42±28		96±14	

Table 12. Mean distance (m) from the reference forest to all vegetation groups. Euclidean distances on spatial coordinates were used to calculate average distance from the centroid.

Trajectory	Vegetation type	Mean distance (m)
Mixed-Broadleaved	Gorse	571
	Em. Natives	624
	Māhoe	924
	Fuchsia	710
Kānuka	Early	441
	Intermediate	422
	Late	369

3.6. *Discussion*

Successional Pathways

The successional pathways described by Wilson (1994) were largely confirmed by this study. They are similar to vegetation development on abandoned land described for kānuka and gorse elsewhere (e.g. Lee et al. 1986; Sullivan et al. 2007). The only modification to Wilson's description was the split of the mixed-broadleaved forest into two different types reflecting the two dominant species present. It remains unknown, if these two stages will gradually converge into the same successional path or if they remain separated with different climax forests.

Results of this study suggest that successional time frames anticipated by Wilson differ for the research area. Wilson expected that the climax forest (beech forest) would be reached by 2050 in sites classified in 1994 as late kānuka forest (in 56 years). The results of this chapter suggest that much longer time frames will be needed. The late kānuka forest is still (2012, 18 years later) distinctly dissimilar to the beech forest, with limited beech and podocarp trees (dbh > 5 cm) present. Regeneration of late successional tree species, even though present throughout the kānuka forests, are at low abundances. Interestingly podocarp regeneration (mainly *P. laetus*) is more abundant than beech seedlings and saplings. The same was observed for the reference forest, podocarp regeneration being much more abundant than beech. This might be a result of light availability, as *P. laetus* has an intermediate shade resistance (Smale & Kimberley 1993) whereas *F. fusca* is a very light demanding species that competes very poorly with other species, and hence requires larger gap sizes to establish (J A Wardle 1984). Another reason could be that regeneration of *F. fusca* might have been underestimated because of its clumped nature (tree fall gap). There is already some indication that the kānuka forest might eventually develop into a forest dominated by either beech or podocarps. If and when these saplings can outcompete the dense layer of broadleaved species underneath the senescent kānuka trees remains to be seen.

The mixed-broadleaved forest types show hardly any indication that they will develop into another successional phase, as regeneration of late successional species is almost completely absent. Hence, Wilson's (1994) prediction that podocarps will be widespread by 2050 and even begin to overtop the mixed-second growth forest seems at this stage to be unlikely. It has been hypothesized that kānuka forest will more readily develop into beech forest because of a shared mycorrhiza which enhances the phosphorus uptake (Baylis 1980; Dickie et al. 2012). Kānuka forests were located in a much closer proximity to the old growth beech forest patches, and with that to seed sources, than the mixed-broadleaved forests in the study area. It is therefore difficult to disentangle if kānuka indeed promotes regeneration of beech or if distance to seed source is the determining factor. This is especially so because the wind-dispersed *F. fusca* has been noted to be extremely slow to colonise adjacent areas. Among suggested reasons are restricted dispersal range because of relatively heavy seeds and limited establishment due to its dependence on mycorrhizal fungi (Baylis 1980). In contrast, podocarps are bird dispersed and their dispersion has been shown to be linked to tree height (provision of perching sites), with tree size becoming

more important with distance to seed source (J Roger Bray et al. 1999). A sufficient tree/shrub height, as observed by Bray et al. (4.5-5.6m), is already being supplied by mature gorse shrubs (up to 4.5 m). Bird numbers and species present in Hinewai are also thought to be sufficient for adequate seed dispersal (Wilson 1994). Moreover, thin-barked tōtara seeds are rather small (ca. 5mm ∅) and easily dispersed by common birds such as black birds (*Turdus merula*) and silvereyes (*Zosterops lateralis*) (Williams & Karl 1996). Mean distance for seed dispersal by silvereyes has been shown to be around 90 m from seed sources (Stansbury 2001). However, almost all broadleaved tree species present in the senescence phase of gorse or in the mixed-broadleaved forests are bird dispersed. It is therefore unlikely that seed dispersal per se is the limiting factor for podocarp spread. As the podocarp density is rather low in reference stands, adequate seed production or the sex ratio of these dioecious trees might be an issue.

In New Zealand the extent of podocarp regeneration under gorse or kānuka varies between studies. For example, Miller and Wells (2003) noted that *Podocarpus tōtara* readily established in gorse in river terraces in south Westland. Abundant podocarp regeneration (i.e. *P. laetus*) under a mānuka (*Leptospermum scoparium*) -kānuka forest was observed by Bray et al. (1999) in Golden Bay, New Zealand. Sullivan et al. (2007), on the contrary, found hardly any podocarp (*Dacrycarpus dacrydioides, P. laetus, Prumnopitys taxifolia*) seedlings under gorse or kānuka stands (200 – 5000 m from seed sources) for similar successional stages as observed in this study.

The regeneration mechanisms of tree species can be complex and influenced by a wide range of variables and site factors. As this question was not explicitly addressed in this study no further conclusions can be drawn.

Quality and Limitation of the Hinewai Chronosequences

Even though every effort was made to ensure that chronosequence assumptions were met, some limitations could not be avoided. First, the successional time frames investigated within this study was shorter than the lifespan of some of the dominant species (Table 4). The age limit for the dominant trees of the mixed-broadleaved forest (māhoe and fuchsia) is not known, but they have been observed to live for at least 100 years Bray (1989). The late successional species, red beech can live up to 500 years and thin-barked tōtara has been estimated to reach at least an age of about 900 years (Ogden 1978; Wells 1972). Secondly, it

remains unclear which climax forest type both chronosequences will finally reach. For the kānuka forest, Wilson's (1988, 1994) prediction that beech will form the climax stage might be still reasonable. However, his prediction that the mixed –broadleaved forest in the research area will evolve into a beech dominated forest remains less certain. However, as there are only a limited number of later successional species present in the research area, it is very likely that it will eventually turn into a podocarp or beech forest. The suggested time frames, however, until climax forests stages are achieved (around 50 years) will be much wider.

It was also impossible to hold the degree or kind of anthropogenic disturbance constant between plots, due to small-scale differences in site management. As a result, speed of successional processes may vary considerably among sampling plots. To overcome this issue in subsequent chapters, development of ecosystem attributes are often modelled along successional stages rather than on progressing recovery time. Despite the issues stated above, the sequence of successional stages was determined by aerial pictures and confirmed by NMDS plots. It is deemed therefore reasonable to test the development of selected ecosystem attributes across them. This is especially so as it is the overall trend rather than the absolute change that is of interest. The use of the beech forest as a reference to evaluate restoration progress is possibly more controversial. For the kānuka forest, which already shows a recruitment of beech and podocarps, this reference seems to be reasonably appropriate. One could suggest that even the broadleaved forest will be eventually dominated by either beech or podocarps due to limited possibilities for other species. However, it remains uncertain, which late successional species will be the dominant one or in what time frame that will be the case. It is disputable to compare compositional similarity of species between the mixed-broadleaved forest and the beech forest. The comparison of structural elements should still be valid, as old growth forests often display common characteristics such as high basal area of larger trees and high deadwood volume and size (sensu Bauhus et al. (2009) for a discussion). Furthermore, the reference forest, as in many restoration projects, is used as guide only, to obtain an indication of the overall progress along the succession.

3.7. *Summary*

The two major successional pathways and stages have been verified for the research area. Limitations of these chronosequences arise mainly from a relatively short observation time frame (87 and 120 years) and the uncertain climax states. However, the time frames examined here are still larger than in many related studies which seldom cover more than a few decades (L. R. Walker et al. 2010). This chapter showed that compositional development can indeed be difficult to forecast, especially in terms of time frames and endpoints. Suganuma and Durigan (2015) dismissed compositional elements as being too unpredictable to be used as indicators of restoration success in tropical forests. Others argued that compositional attributes in particular are important indicators and should always be used in combination with other ecosystem elements (Brancalion & Holl 2016; Leighton Reid 2015). General trends, at least for the low diversity ecosystems observed here, can be seen using ordination plots or multivariate MANOVAs. Reid (2015) pointed out that compositional analysis does not have to stop at similarity/dissimilarly matrices. It is not only important to establish if the restored forests diverge relative to the reference but also in which species they differ. Analysis of key compositional elements such as presence of characteristic species of the reference forest (e.g. late successional, threatened, or old growth species) in the restored sites will add more meaning to any assessment of restoration success. In particular, the presence of late successional species in different life stages seem to be a very useful attribute to assess ecosystem condition and predict future ecosystem development.

Chapter 4
Assessing Restoration Success with Forest Structural Measures

4.1. *Abstract*

Assessment of restoration success based on structural attributes in forests has been criticized because the underlying assumption of surrogacy for faunal species and ecosystem function is often not explicitly tested. It has been suggested that structural attributes hold low information content in comparison to diversity measures for restoration purposes. However, without fulfilling the habitat requirements for wildlife, it is unlikely that these species will colonize the restoration site or persist if they do. Quantifying forest structural development is therefore an important task for assessing restoration success in forested environments. For the purpose of forest restoration, structural attributes should be able to efficiently differentiate between major seral stages and assess habitat quality. Development of structural attributes over successional stages is described in the forestry related literature, but their usefulness for describing restoration success has gained less attention. Similarly, choice of measures for assessing structural diversity, which have been shown to be closely associated with habitat quality in forests, has largely been limited to production forestry settings. To assess whether these forestry measures are useful for assessing restoration success, I tested (i) the consistency and strength of trends shown over increasing recovery time, (ii) the correlation among measures, and (ii) the ability of discriminating between early and late successional stages, in a restoration project. Results indicate that simple measures like basal area or stem density can be used to assess the progress of succession and, with that, ecosystem recovery. These attributes are most effective if examined for different tree sizes reflecting consecutive life stages of trees, or separately for each dominant species. Tree size diversity indices, frequently applied to assess structural diversity such as the Shannon index and the Gini coefficient did not effectively distinguish between seral stages. This might be a consequence of treating all diameters or diameter classes as being of equal importance. This effect could not be overcome by using basal area for these indices to assign higher values to larger tree sizes. Simple attributes based on absolute differences were found to

outperform the indices mentioned above, namely mean diameter and the standard deviation of the tree diameter.

4.2. *Introduction*

Measures of vegetation structure are commonly applied to assess restoration success in forests (Ruiz-Jaén & Aide 2005a). Advantages are their easy and rapid measurement and the relative lack of seasonal variation (Gibbons & Freudenberger 2006; Ruiz-Jaén & Aide 2005a). Specific structures are also commonly associated with different successional stages of forests; thus can be used to differentiate between seral stages in vegetation development and could be effective to assess restoration success (Bauhus, Puettmann, & Messier, 2009; Franklin & Van Pelt, 2004).

The structure of a forest influences key ecosystem functions such as the nutrient cycle, while structural diversity in particular has been shown to affect faunal species richness and diversity (Brokaw & Lent 1999; Ferris & Humphrey 1999; McElhinny et al. 2005). Consequently, structural attributes have been used as surrogate measures to assess the more difficult to measure ecosystem functions and faunal diversity (Ferris & Humphrey, 1999; Franklin et al., 2002; McElhinny et al., 2005; Truman P Young, 2000). This approach has been frequently criticized for being over simplified, assuming the surrogacy value of vegetation structure rather than testing it, potentially missing impeding factors influencing ecosystem function and diversity (Block et al. 2001; Ehrenfeld & Toth 1997; Hilderbrand et al. 2005; Suding 2011). In addition, structural attributes have been suggested to hold lower information content than biodiversity and compositional measures for the assessment of restoration success (Wortley et al. 2013). However, without achieving suitable habitat quality first, which is strongly entangled with vegetation structure and successional stage in forests, faunal species are unlikely to colonise or persist in the long run.

There is still considerable debate about which ecosystem attributes are most suitable to describe forest structure, particularly structural diversity (McElhinny et al. 2005). Most of these attributes have been evaluated in production forestry settings, which have a different focus than restoration projects. Even though these attributes are commonly applied, their usefulness for evaluating restoration success is not entirely clear. For restoration settings, structural attributes have to distinguish reliably between major successional stages from stand initiation (e.g. restoration plantings) to old growth forest to monitor

restoration progress (i.e. show strong trends over time). They should also be able to assess habitat quality, especially with respect to a reference system that might be at the same successional stage, but will most often be an old growth forest.

Habitat quality can be assessed by investigating the presence of key structural elements such as coarse woody debris and habitat trees, or by evaluating vertical and horizontal diversity in forests. All these structures are general characteristics of old growth forests. Horizontal diversity is often evaluated by using diameter based indices or measures. The advantages of diameter related attributes are the ease of measurement and their high correlation with other tree size measures (Lexerød & Eid 2006; Varga et al. 2005). Diversity measures based on tree height or vegetation layers have been used to evaluate the vertical structure in forests (Parker & Brown 2000; Ruiz-Jaén & Aide 2005a; Van Den Meerssehaut, Diego Vandekerkhove 2000). Attributes utilizing cover percentages of vegetation layers seem to be the most feasible measure in terms of ease of measurement, but their suitability for assessing recovery of forest structure and with that restoration success remains to be tested.

To provide a more solid basis for the application of forest structural attributes in restoration projects, the suitability of structural attributes commonly used for describing stand structure, key habitats, and tree size diversity were investigated in this study. A chronosequence approach following two successional trajectories (kānuka and mixed-broadleaved forests) on abandoned farmland was applied to test a range of structural attributes in terms of their (i) consistency and strength of trends shown over increasing recovery time, (ii) their correlation with each other, and (iii) their ability of discriminating between early and late successional stages.

4.3. *Methods*

4.3.1. Study Site and Research Design

See Chapter 3 pages 25 - 29 for a comprehensive description of the study site and the research design. Successional stages along the vegetation trajectories are described in Chapter 3 pp: 35 - 37.

4.3.2. Ecosystem Attributes Tested

A range of attributes describing (1) stand structure, (2) key habitats and (3) tree size diversity were investigated.

Stand Structure
Frequently applied structural measures were selected to assess forest development including stem density and basal area (Franklin et al. 1981; Spies & Franklin 1988), canopy cover (Bauhus et al. 2009), height (Castro-Luna et al. 2007) and mean tree diameter (Franklin et al. 1981; Spies & Franklin 1991).

Basal Area and Mean Diameter

Measurements for diameter based attributes were collected in two circular concentric plots, having a radius of 6 and 12 m. Tree dbh (dbh = diameter at breast height) was measured at 1.4 m height using a diameter tape and species identity was noted. Within the 6 m plot, trees ≥ 1 cm dbh were recorded and a radius of 12 m was used for trees ≥ 20 cm dbh. Basal area and mean diameter were calculated by using only trees ≥ 5cm dbh; trees with a smaller diameter are regarded as regeneration (saplings) and not as established trees. Both plots were extrapolated to hectare values, subsequently aggregated and basal area ($m^2\ ha^{-1}$) and mean tree diameters (cm) were calculated.

In order to explore the underlying trends for basal area in more detail, tree species were congregated into two groups based on their absolute community dominance: dominant and subordinate. According to total abundances, dominant species were defined to be kānuka (*Kunzea robusta)* in the kānuka forests and māhoe (*Melicytus ramiflorus*) and fuchsia (*Fuchsia excorticata*) for the mixed-broadleaved forests.

Stem Density

Stems per hectare were derived similar to basal area and mean diameter, but using only the number of stems encountered (stems ha^{-1}). For part of the

analysis, this data set was also split into dominant and subordinate species (as defined above).

Canopy Cover

Within each 12 m plot, canopy cover was visually estimated to the nearest 10 % using a canopy cover scale from Landcare Research (Hurst & Allen 2007). Canopy being defined for the purposes of this study to be the highest vegetation tier dominated by tree species within the sampling plot.

Canopy Height

Canopy height in meters was obtained by measuring the heights of at least five trees per sampling plot, using a Vertex 3 clinometer. The trees were selected based on their social status within the canopy. According to individual tree height and crown expansion in relation to the surrounding trees five main crown canopy classes were distinguished (first described by Kraft 1884; adapted by Pretzsch 2009 pp. 154–156): predominant (I), dominant (II), codominant (III), subdominant (IV) and suppressed trees (V). Only trees belonging to either class I or II were measured.

Regeneration

Regeneration density can be a characteristic of old growth forests (Dodson et al. 2014) and has been used to assess restoration impediments (E. White et al. 2004) and success (Parrotta & Knowles 1999). Due to the high variation in seedling densities, four sampling subplots of 1 m radius were established 6 m East, South, West, and North of the main plot centre. A 2 m ranging pole, having 0.5 m markings was used to established plot boundaries. Within the seedling plot, all tree species < 140 cm height were identified and counted. Mean values across these four subplots were used for the analysis.

Key Habitats

Dead Wood

Dead wood was included as its volume, size and decay class distribution are characteristics of many mature forests (Bauhus et al. 2009; Perry et al. 2008). Two forms of woody debris have been estimated for the purpose of this study: snags and coarse woody debris. Coarse woody debris (CWD) and snags (i.e. standing dead trees) were sampled within the 12 m radius plot. Middle diameter and length were measured for every log over 5 cm diameter at the larger end. Snag height and middle diameter were recorded when the dbh was ≥ 20 cm. Heights were measured using the Vertex 3 and middle diameters were visually

estimated. Accumulated plot values were used for snag and coarse woody debris volume (m^3 ha^{-1}); mean diameter of CWD was calculated per plot.

Leaf Litter

Leaf litter volume was chosen as leaf litter and soil organic matter dynamics play a key role in decomposition and nutrient cycling. Both represent diversity and functional hot spots in forest ecosystems (Hansen 2000). Consequently, studies evaluating restoration success occasionally include measures of leaf litter structure such as: cover percentage, number of litter layers or litter depth (Ruiz-Jaén & Aide 2005a). Leaf litter volume was sampled 2 m North and South from the plot centre. Within a 25 cm x 25 cm metal quadrat all leaf litter was removed until the mineral soil was reached, subsequently the volume was measured with a measuring jug in cm^3. Leaf litter volume was averaged across the two subplots for the analysis.

Structural Diversity

Horizontal Diversity

All attributes tested were based on tree diameter measurements and have been used as indicators for tree size diversity.

Standard Deviation of the Mean Diameter

The easiest measure applied in this study; it has been suggested to be a good indicator of tree size diversity and to correlate well with more complicated indices, is the standard deviation of the mean diameter (s_{dbh}) (Franklin et al. 1981; Neumann & Starlinger 2001; Spies & Franklin 1988).

Shannon Index

The Shannon index (H'_d) was chosen as it is frequently applied to assess structural complexity in forests (Lexerød & Eid 2006; Valbuena et al. 2012). It is based on the proportion of basal area per diameter class. Basal area was used instead of number of individuals to add more weight to larger trees sizes (Table 13). A bin size (class width) of 5 cm was used for the diameter classes and the lower limit is given in figures (e.g. class 5 = 5 cm - 9.9 cm dbh). The lowest possible value of H'_d is zero; all trees are in the same diameter class and the maximum value is defined by the natural logarithm of the total number of diameter classes observed per plot.

Gini Coefficient

The Gini coefficient (*GC*) has been suggested to outperform other measures of tree size diversity in forestry management settings (Lexerød & Eid 2006). It requires ranking of all trees per plot in ascending order according to their size. The so-called Lorenz curve shows the cumulative proportion of both individuals and their basal area against each other. The line of equality shows the theoretical case where all individuals have the same basal area. The Gini coefficient is then the relationship of the area between the line of equality and the Lorenz curve as the numerator and the total area below the line of equality as the denominator. It is thus a measure of inequality and ranges between zero and one; one reflecting total inequality between individuals.

Vertical Diversity

To assess vertical stratification within the sample plots, number and kind of vegetation tiers present within the 12 m circular plot was recorded. A vegetation tier was defined to have a cover percentage of at least 20 % and was named after the dominant plant group (e.g. ferns, shrubs, trees). Vertical structural diversity was then computed using Shannon's formula (H'_{TC}), modified to assess vertical layering as applied by Fierke and Kauffman (2005). Total cover percentages for up to three vegetation tiers were used; reflecting fern, shrub and tree layer.

Table 13. The different structural indices and measures used in this study are given with their formula and references.

Div.	Indices	Formula	Range	Reference
Horizontal	Gini index	$GC = \frac{\sum_{j=1}^{n}(2j - n - 1)ba_j}{\sum_{j=1}^{n} ba_j\,(n-1)}$	[0,1]	(Gini 1912; Lexerød & Eid 2006; Valbuena et al. 2012)
	Standard deviation of dbh	s_{dbh}= SD of mean dbh	[0, ∞]	(Spies & Franklin 1991)
	Shannon index	$H'_d = -\sum_{i=1}^{S} p_i In_{p_i}$	[0,In(S)]	(Shannon 1948; Staudhammer & LeMay 2001)
Vertical	Vertical structural diversity	$H'_{TC} = -\sum_{i=1}^{S} p_i In_{p_i}$	[0,In(3)]	(Fierke & Kauffman 2005; Shannon 1948)

For H'_d ,p_i is giving the proportion of basal area (m^2 ha^{-1}) for diameter class i in relation to the total plot basal area (m^2 ha^{-1}) and S indicates the total number of diameter classes present.
H'_{TC} is using respectively p_i for the proportion of cover percentage of tier i relative to the cumulative cover percentages of all tiers, S refers to the total number of vegetation tiers observed in a plot. GC employs j as the rank of a tree in ascending order from one to n, ba_j refers to the basal area for a tree of rank j (m^2 ha^{-1}) and n denotes the total number of trees.

4.3.3. Statistical Analysis

Grouping of Sampling Plots

Even though fuchsia and māhoe dominated forests are compositionally quite different (see Chapter 3), their similarity regarding ecosystem structure was uncertain. In order, to decide whether both vegetation trajectories were significantly dissimilar from each other, a Permutational Multivariate Analysis of Variance (PERMANOVA) was applied. The PERMANOVA was performed for all attributes simultaneously using the Adonis function from the Vegan package. This analysis is analogous to the method described by Anderson (2001). Structural attributes were standardized and Euclidean distances were used to calculate the distance matrix; recovery time was included as a covariate to correct for differences in observation time between vegetation groups. As no significant difference between the fuchsia and māhoe vegetation group means was obtained (*pseudo* $F_{(1,73)} = 0.84$, partial $R^2 = 0.01$, $p > 0.05$, $nPr = 999$), both trajectories were subsequently analysed as one group termed 'mixed-broadleaved forest'. The same analysis procedure found a non-significant difference between Hinewai and the bordering farmland plots for the structural attributes (*pseudo* $F_{(1,73)} = 2.765$, partial $R^2 = 0.02$, $p > 0.05$, $nPr = 999$). Subsequently, these plots were also integrated into the dataset to further enhance statistical power.

PERMANOVA requires the homogeneity of dispersion among groups, which can be tested by using the betadisper function in conjunction with a permutation test (function permutes). For both analyses this test was also non-significant ($p > 0.05$, $nPr = 999$), hence the variance in the groups was equal.

Attribute Behaviour over Time

Attribute development over increasing recovery time was studied by using standard linear regression methods. This included appropriate data transformations to satisfy linear model assumptions (see Appendix 2 for transformations applied; Appendices 3+4 for scatterplots on raw data). A quadratic term was added to the model, if significant in the model output. Model results were afterwards transformed into Pearson's coefficient (r_p) to generate a summarizing correlogram, which directly relates to the observed model R^2. In addition, to unravel the relationship between structural attributes, a Spearman's rank (r_s) correlation coefficient was calculated. Due to the non-parametric, rank based nature of this test, no data standardisation was necessary. Resulting *p*-values were corrected for multiple comparisons by Holm's method (Holm 1979). At last, to enable comparison of attribute response shapes over recovery time,

they had to be relativized to a common reference system, the beech forest. Regression model outputs were transformed into relative values compared to the reference forest means. That way, it was also directly evident how secondary forests ranked, when the modelled results for the highest observed sampling plot age were compared against the reference site values.

4.4. *Results*

4.4.1. Attribute Relationship with Recovery Time

All but two measures (snag volume and its mean diameter in the mixed-broadleaved forest) displayed a significant trend over increasing recovery time (Figure 7, Appendix 2). The weakest and most inconsistent trends ($r_p < 0.5$) were observed for regeneration density (tree height < 1.4 m, trees ha^{-1}), CWD, and snag volume (m^3 ha^{-1}). Canopy cover (%) and stem density (stems ha^{-1}, dbh ≥ 5cm) showed a negative trend with recovery time for the kānuka trajectory, as kānuka reaches its age limit after 80 - 150 years, with the canopy beginning to open up (Burrows 1973). A strong positive trend was evident for the vertical diversity index (H'_{TC}) in the kānuka trajectory, which was slightly less distinct in the mixed-broadleaved trajectory. Leaf litter volume was in both vegetation trajectories negatively correlated with recovery time. This is probably caused by the diminishing dominance of gorse (*Ulex europaeus*) in the mixed-broadleaved trajectory and the increase of tree species having a more readily decomposing leaf litter than kānuka in the kānuka trajectory. A medium ($r_p > 0.5$) to strong ($r_p > 0.75$) positive trend was apparent for the vertical and horizontal diversity measures.

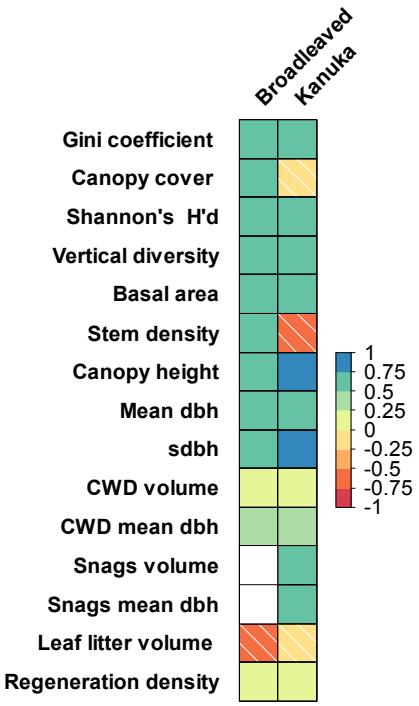


Figure 7. Structural attribute correlation with increasing recovery time. Shown are the regression results with appropriate data transformation and quadratic terms (see Appendix 2 for details). R^2 values are depicted; the direction of the relationship was determined by the positive or negative value of the regression slope. Non-significant results ($p > 0.05$) are left blank. For analysis of diameter related measures, all tree dbh > 5cm have been used. CWD depicts coarse woody debris.

Closer inspection of attribute development over recovery time, using different subsets of the tree data set, elaborated the underlying trends especially for basal area and stem density. The importance of choosing appropriate data subsets can be seen in Figure 8. Basal area was analysed using different dbh thresholds as well as species dominance groups (Figure 8 B + C). The overall basal area (using all trees > 1 cm dbh) for the kānuka trajectory seems to indicate a steady increase over time. Inspecting subsets of the tree data showed that kānuka grew over time into the > 20 cm dbh classes with no further recruitment, as stems under 20 cm were largely absent at the end of the observation time (Figure 8 C). The subordinate broadleaved species gained increasing dominance in this vegetation trajectory, thus clearly signalling the transition into the next successional phase. The increase in stems in the dhb class 1 -5 cm was a result of broadleaved species being recruited (Figure 8 C + D). The mixed-broadleaved trajectory, in contrast, seemed to be in its thinning phase, dominant species displayed a steady increment, especially within the > 20 cm dbh class, whereas the slope for stems under 20 cm seemed to decrease (Figure 8 A).

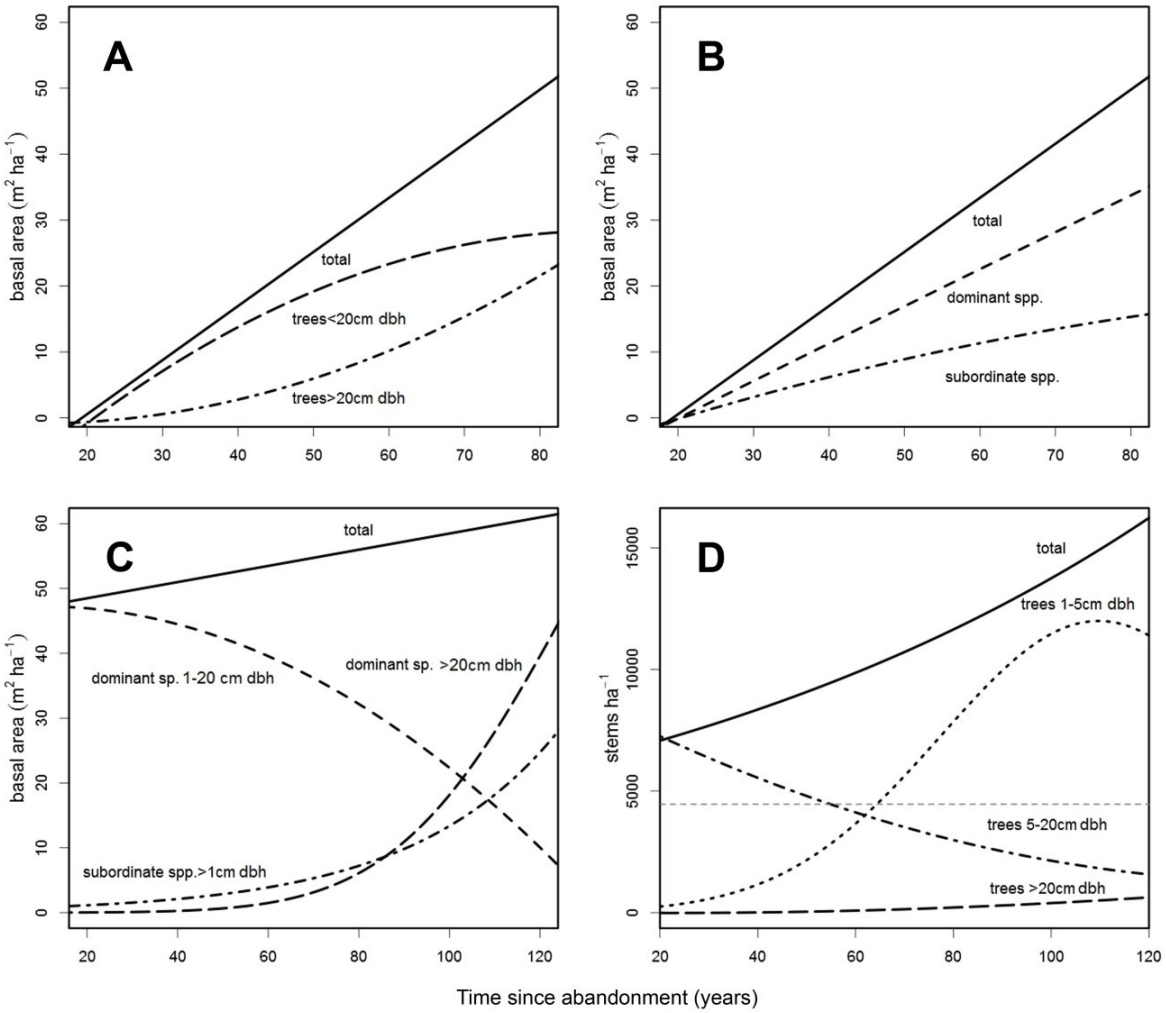


Figure 8. Linear regression model results, showing the modelled mean basal area (m^2 ha^{-1}) over increasing recovery time for the mixed-broadleaved trajectory (A, B) and kānuka (C). D depicts regression lines for stem density in the kānuka trajectory across all tree species. Total stem density contains all trees ≥ 1 cm dbh.

To explore the behaviour of attributes over recovery time simultaneously, it was necessary to scale model lines gained by the linear regression analysis, relative to the mean of the reference forest (Figure 9 A). Monotonic responses were observed for all but one attribute within the mixed-broadleaved trajectory (leaf litter volume). All measures showed a monotonic shape for the kānuka forest. Kānuka displayed opposite trends in some attributes in comparison to the mixed-broadleaved trajectory. For example, canopy cover showed a steady decline (Figure 9B), as does stem density for trees ≥ 5cm dbh (Figure 10).

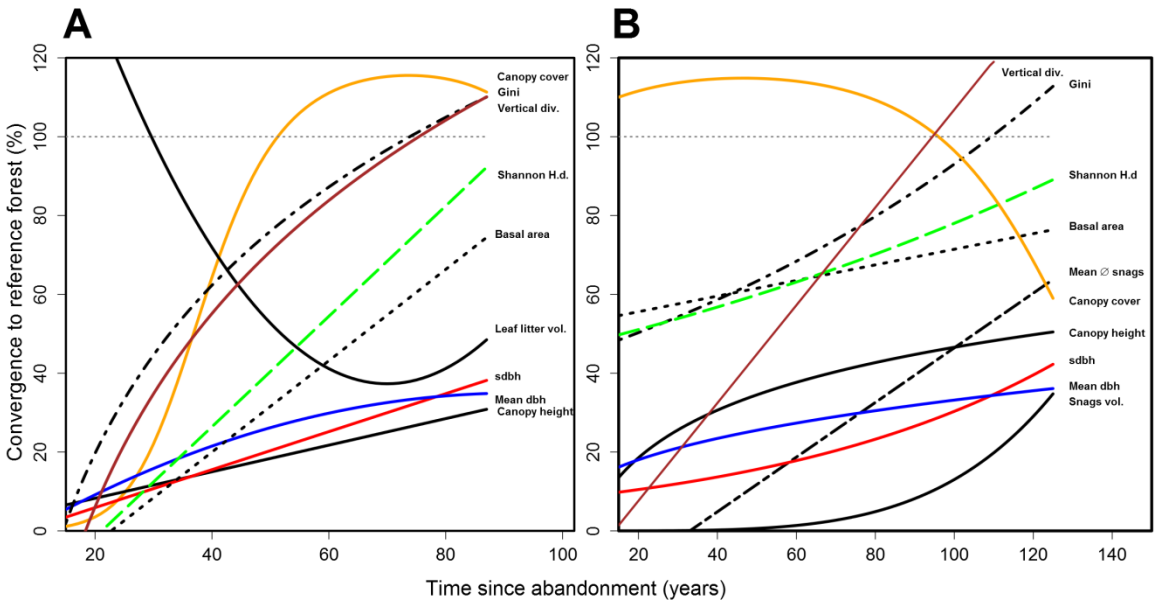


Figure 9. A selection of structural attribute regression lines transformed into percentages of mean reference values for the mixed-broadleaved (A) and kānuka (B) trajectories. All trees ≥ 5cm dbh were used for calculating dbh related measures. See Appendix 2 for details on regression coefficients and measurement units used.

4.4.2. Relationship between Ecosystem Attributes

The relationship between attributes was somehow difficult to assess with correlograms, as most measures showed a weak to strong correlation with recovery time. Correlations observed for different attributes could be therefore a result of cross-correlation with recovery time. However, when a stronger correlation was observed between two attributes than with development time, the correlation might be genuine. This was observed for related measures such as mean dbh and s_{dbh} (Figure 11 A + B). Litter volume was strongly negatively correlated with all other measures within the mixed-broadleaved trajectory. A similar behaviour was observed for stem density in the kānuka trajectory in relation to mean dbh, s_{dbh}, leaf litter volume and regeneration density. For the mixed-broadleaved forest, the scaled response shape of total basal area (m^2 ha^{-1}) over increasing recovery time seemed to be reflected by a similar shape of the structural diversity measure Shannon's H'_d (H'_{TC}) (Figure 9 A). For the kānuka trajectory, total basal area displayed only a very slow increase. This contrasts with all three structural diversity indices that show a steady increase over recovery time. A strong correlation was found between the Gini coefficient and the s_{dbh} for both forest trajectories, which might have been caused by a cross-correlation with recovery time (Figure 11).

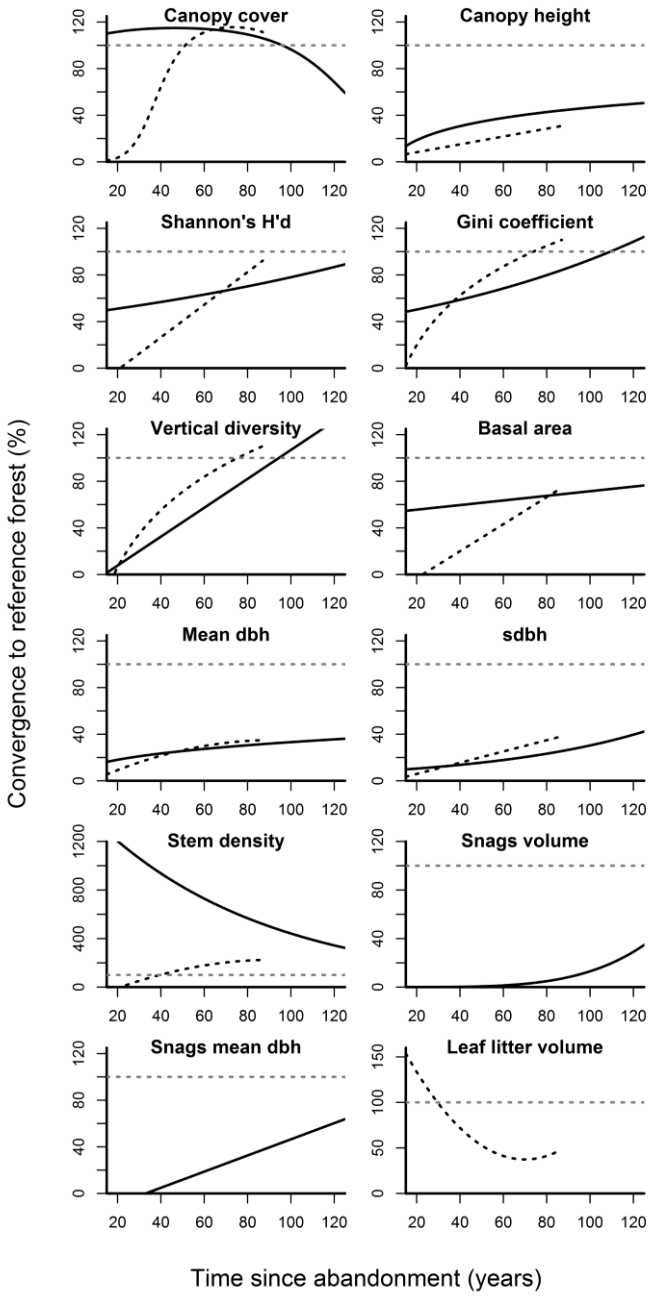


Figure 10. Attribute convergence towards the reference forest. The thick dashed line represents the mixed-broadleaved forest, the solid line depicts the kānuka trajectory and the grey horizontal line is indicating the reference forest mean. Only attributes which showed a significant trend over increasing recovery time and retain an $R^2 > 0.20$ are displayed using regression lines.

4.4.3. Attribute Convergence towards the Reference System

Final values reached in the two early successional forests were compared to an old growth forest (the reference site) to assess attributes ability to distinguish between successional stages. Attribute summary statistics, providing means and standard errors for the reference sites (*Fuscospora fusca* forests), are given in Table 14. Modelled values for the last observed point in time for both successional forests, in relation to reference values, are presented in Figure 10.

In both second growth forests total basal area reached about 75 % of the reference mean and was still accelerating. It was not surprising that reference canopy height was still far off from the modelled value for the two successional forests, as tree species capable of reaching this height were largely absent.

Table 14. Summary statistics for all attributes are provided below for the reference forest (*F. fusca* dominated forest). All dbh related measures are calculated using trees ≥ 5 cm dbh).

Attributes	Mean±SE	Coefficient of variation
Gini coefficient (*GC*)	0.46 ±0.1	0.43
Canopy cover (%)	0.79 ±0.1	0.11
Shannon's H'_d	1.93 ±0.1	0.16
Vertical diversity (H'_{TC})	0.88 ±0.1	0.11
Basal area (m^2 ha^{-1})	82.60 ±4.7	0.26
Stem density (stems ha^{-1})	4460.20 ±788.9	0.83
Canopy height (m)	27.14 ±0.4	0.07
Mean dbh (cm)	42.59 ±3.4	0.38
sdbh (cm)	20.53 ±1.7	0.39
Leaf litter volume (m^3 $plot^{-1}$)	5282.70 ±360.3	0.32
Snags volume (m^3 ha^{-1})	15.03 ±4.6	1.44
Snags mean dbh (cm)	25.69 ±4.9	0.90
CWD volume (m^3 ha^{-1})	21.23 ±6.1	1.34
CWD mean diameter (cm)	22.19 ±2.3	0.48
Regeneration (count ha^{-1})	52518.90 ±4963.7	0.44

Deadwood values were also much lower in kānuka and mixed-broadleaved forest than volumes and sizes observed in the beech forest. Stem density was considerably higher for kānuka and the mixed-broadleaved forest. Somehow unexpected was, that the tree size diversity indices suggested that the two successional forest types were almost equally (H'_d) or even slightly more structural diverse (*GC*) than the reference sites. The mixed-broadleaved forest accomplished reference values for both indices 30 - 38 years earlier than the kānuka forest.

However, according to the s_{dbh} both forest types are still quite dissimilar from the reference (ca. 40 % of the reference values). The mean diameter of the stands also reached only a low level (kānuka, 36 % and mixed-broadleaved 34 %) of the beech forest. In the kānuka forest some form of structural diversity was already reached after 20 years; as mixed-broadleaved forest had to overcome the shrub phase first, it took about 20 (*GC*, s_{dbh}) to 50 (H'_d) years more to display similar values (Figure 12). The mixed-broadleaved forest varied in its response, displaying a positive logarithm shape for $H'd$ and a linear for *GC*. The reference

forest showed a high variation in the Gini coefficient (CV = 0.42) in comparison to the two second growth forest types (CV_{kan} = 0.01, CV_{br} = 0.12) for the last point in time. It also displayed the highest number (13) of diameter classes present in a stand, meaning that H'_d could have reached a theoretical value of 2.6, the mean for reference forest was 1.93. Both successional forests outperformed the reference forest regarding the vertical diversity index (H'_{TC}), with the kānuka forest reaching the highest value.

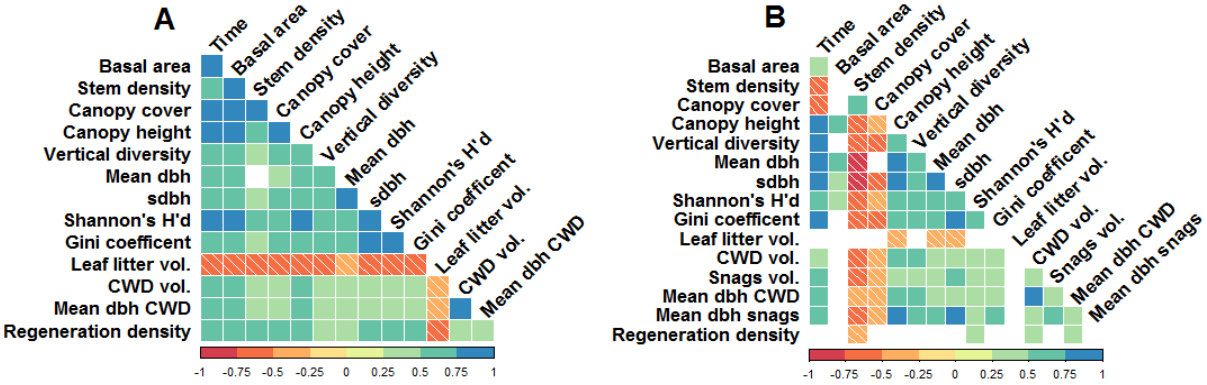


Figure 11. Correlograms using Spearman's rho, showing attribute correlation for the kānuka (A) and mixed-broadleaved (B) trajectory. Non-significant results ($p > 0.05$) are left blank.

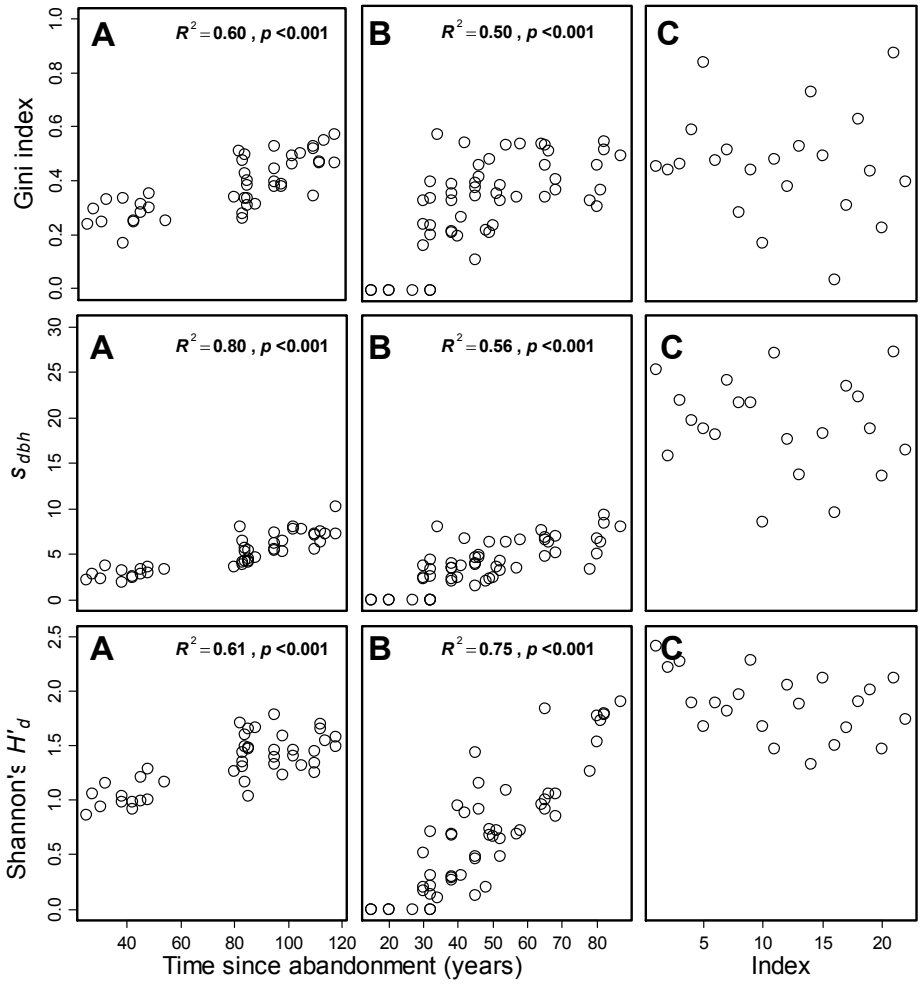


Figure 12. Structural index results for the kānuka (A), mixed-broadleaved (B) and reference forests (C).

4.5. *Discussion*

Almost all structural attributes investigated displayed a medium to strong response to increasing recovery time. The two exceptions were regeneration density and the two deadwood categories. It is well known that regeneration abundances can be dependent on a large set of site specific factors acting at different scales such as canopy openness, soil fertility, and moisture as well as distance to seed sources (Grubb 1977). These factors then result in a mosaic of densely regenerating patches and gaps at a very small scale (Hessenmoeller et al. 2013). Even though four subplots were used to account for the high in-plot variation in regeneration densities, this might have been insufficient to sample regeneration abundances representatively.

The weak trends observed for coarse woody debris in both forest trajectories can be attributed to the relatively short observation time frame (mixed-broadleaved forest = 87 years, kānuka forest = 125 years). The increasing snag volume over recovery time in the kānuka trajectory is caused by the dieback of mature kānuka trees which typically do not live much beyond this time frame (Burrows 1973), while dieback of māhoe and fuchsia individuals has not yet occurred. It is no surprise that deadwood quantities (volume) and qualities (diameter as a proxy) differed greatly between the old growth forest and the relatively young second growth forest types. Development of larger sizes of deadwood can take a long time, up to centuries (Kanowski et al. 2003; Sturtevant et al. 1997; Vandekerkhove et al. 2009) on abandoned land or previously managed stands and is therefore regarded to be a characteristic of old growth forests (Bauhus et al. 2009).

Overall, the temporal trends displayed by the structural attributes in both forest trajectories, are typical for early successional forests; high initial stem densities and rapid canopy closure, small tree dimensions and a slow but steady increase in coarse woody debris and snags (Franklin et al. 2002). There are however, differences between the two successional pathways. Both forests types evolved from pasture followed by a phase dominated by light demanding woody pioneers, native (kānuka*)* or introduced (gorse) (Wilson 1994). The early pioneer stage dominated by gorse was generally succeeded by the next sere characterized by broadleaved trees in less than 40 years. After 87 years, the mixed-broadleaved forest is in its biomass accumulation/competitive exclusion stage, indicated by still increasing stem density and high stem numbers in low diameter classes (Appendix 5). Kānuka forest however, shows a slow development for basal area,

a negative trend for canopy closure and stems over 5cm dbh, coupled with an increase in advanced regeneration (dbh = 1 -5 cm). This is a result of the first tree cohort (kānuka) slowly diminishing after 125 years and being replaced by a more shade resistant second tree cohort (broadleaved trees such as mountain-five-finger (*Pseudopanax colensoi*), māhoe).

As both forest types are clearly still in an early successional stage, the results obtained by the structural diversity indices were unexpected. Both secondary forests either accomplished or came very close to reference values for the Gini and H'_d indices, contrary to the standard deviation of the mean dbh. However, even though all three indices are based on dbh measurements, they do focus on different aspects of structural diversity. The Gini coefficient, as a measure of size inequality across all tree individuals, assigns the highest values towards stands displaying a reversed-J curve diameter distribution. The lowest values are calculated for shapes that follow almost normal (bell-shaped) diameter/basal area distributions (Bílek et al. 2016; Duduman 2011; Lexerød & Eid 2006). The diameter distribution of the reference forest resembles a bell-shape. Whereas, both secondary stands display a positively skewed diameter curve, which is similar to the reversed-J curve (see Appendices 5 and 6); hence, they reached higher scores for the Gini coefficient. Noticeable is the high variation in the index results for the reference forest. This is probably a result of the mosaic of gaps with advanced regeneration present throughout the reference sites, rather than a scale issue (i.e. plot size not adapted to tree sizes sampled); to account for scale issues concentric plots with different plot radii were chosen. Affected plots show a negatively skewed basal area distribution rather than a bell shape and with that receive higher Gini values.

The Shannon index (H'_d) as a measure of tree size diversity, accounts for the diameter range and the evenness of basal area distribution across it. Lexerød and Eid (2006) found that the Shannon was more effective than the Gini index in discriminating sites with a higher evenness across diameter classes. It reaches higher values when basal area is distributed more evenly across diameter classes or when the number of diameter classes increases (Staudhammer & LeMay 2001). The mixed-broadleaved forest was steadily growing into higher diameter classes over time; hence, the linear increase in H'_d index results. The known slow diameter growth (Smale et al. 1995), which stagnated over the last observation period as kānuka reached its maximum diameter on these sites, leads to a slow increase of dbh classes present; hence, the flat curve observed for H'_d kānuka

index results. The potential sensitivity of H'_d towards the choice of diameter class sizes has been noted repeatedly, but no recommendations have been given regarding bin size (Lexerød & Eid 2006; Staudhammer & LeMay 2001; Varga et al. 2005). The maximum number of diameter classes found was 13 and relates to H'_d max.: 2.56. Even though the reference forest contained on average more diameter classes than the two second growth forest types, it also showed the largest variation in them. The between-plot variation in the reference (red beech) forest, in addition to a relatively high number of diameter classes observed in the successional forests, is therefore likely to have caused the high divergence to the reference forest.

In contrast to the relative attributes discussed above, attributes based on diversity measures represent absolute differences within tree sizes (mean dbh) and their variation (s_{dbh}). Both indicate that the two second growth forests are still quite dissimilar from the reference. Even though the Gini index has been successfully used to discriminate stands under different silvicultural management, it has frequently been found to fail to differentiate natural from managed forests (Bílek et al. 2016; Rouvinen & Kuuluvainen 2005). This might be a result of the lower values assigned to bell shaped basal area/diameter distributions. The Gini index might therefore be more useful in silvicultural settings targeting uneven-aged stands, where often the goal is to achieve stand structures that reflect (not necessarily natural) reversed – J curves (O'Hara & Gersonde 2004). This diameter distribution has been thought to reflect old growth forests, but it has been shown that this is not necessarily so (Coomes & Allen 2016). For example, in the light demanding red beech dominated reference forests either a normal or a left skewed bimodal diameter curve would be expected (or right skewed bimodal for the basal area distribution) as shown in Appendix 5 and 6; caused by the time lack in regeneration (John A Wardle 1984). Therefore, results of indices evaluating *relative* unevenness of basal area or diameter distribution across trees (e.g. Gini, Shannon index) should be interpreted with special caution. Gini and Shannon indices reflect the relative inequality across size classes, which could have a rather low absolute diameter range (e.g. from 2cm up to 15 cm) or not (e.g. 5cm - 60 cm). Therefore, they do not tell us anything about the magnitude of differences in diameter classes present. On the other hand, a wide *absolute* diameter range and especially the presence of larger tree dimensions has been effectively connected to an increase in wildlife habitat and are known to be indicators of old growth forests (Franklin et al. 1981).

The easiest measures of tree size and its diversity (i.e. the mean diameter and its standard deviation) seem to have the highest discriminant ability between successional stages. They might have also the highest surrogate value for habitat value/quality, as generally larger tree sizes are attributed to higher habitat diversity. However, Spies and Franklin (1991) found that the mean diameter did not distinguish well between different successional Douglas-fir forests, as the same mean diameter or standard deviation of diameters can occur for different diameter distributions. It is therefore always advisable to inspect the underlying diameter distribution.

Both successional forests came close or reached reference values for the vertical diversity index. A study investigating structural changes along a riparian forest successional gradient also found low discriminate ability between early, mid and late forests for this index (Fierke & Kauffman 2005). The vertical diversity measure H'_{TC} tested in this study was probably too simplified as it did not take into account the height and width of the tiers inspected. There are not many indices available in the literature to quantify vertical structure in forests (Neumann & Starlinger 2001). A better indication of vertical layering might be obtained by a method applied by Ruiz-Jaén & Aide (2005b), who measured heights of all woody plants >1cm dbh along a transect.

The other important aspect of spatial arrangement of trees (i.e. horizontal structure) could not be quantified in this study, due to time constraints. Recently, Dickinson et al. (2016) suggested that this feature could be easily assessed by quantifying patch density and sizes in forests using a spatial modelling approach based on aerial imagery. However, more research is needed here to test, develop or improve methods to assess vertical and horizontal layering in forests.

4.6. *Summary*

This study showed that simple measures like basal area or stem density can be used to monitor the progress of succession/recovery and with that increasing habitat quality. These attributes seem to be especially effective if examined for different tree sizes reflecting consecutive life stages of trees or incorporating compositional features such as dominance groups or individual species.

A limitation of this study was its relatively short observation time (87-125 years) in comparison to successional time spans of old growth forests in this system (e.g. according to Ogden (1978) red beech can live at least 500 years).

As a result, some attributes characteristic of old growth forests, such as formation of larger amount and dimensions of dead wood, will take centuries to develop. However, life spans of most restoration projects are currently much shorter than the observed 87-125 years here (e.g. Bull et al. 2013).

Formation or behaviour of structural attributes is linked to early, mid and late successional stages in forests, and thus have to be used accordingly. Development patterns over time for these attributes are generally well known and are straightforward to interpret and predict. However, they should not be used in an oversimplified manner. Canopy closure is only one of the first steps of stand development and does not necessarily reflect restoration success. Assessment of structural diversity using either relative inequality between tree sizes (Gini) or their diversity (Shannon) might not be the most suitable choice for restoration settings. Both have not been effective in discriminating between successional stages and they treat all diameters/diameter classes as being equally important. Restoration projects usually associate increasing habitat quality with larger tree sizes and absolute differences in their diameter ranges, which have been used as surrogate measures for faunal habitat (Parkes et al. 2003). The mean diameter together with its standard deviation is easy to measure and interpret and seem to be more useful in a restoration context.

In summary, some attributes (i.e. basal area, stem density, mean diameter and its standard deviation) will be universally useful for assessing or monitoring progress towards restoration success. The usefulness of other attributes, which are characteristic for certain successional stages (i.e. volume of snags), will depend on the successional development that occurs at the particular site. For long term monitoring, it might be best to apply a progressive framework, adjusting attribute selection and values according to the successional stage of the restoration project. Reference values should be obtained, if possible, by sampling across a range of natural forests with comparable successional stages present. The main successional stages along the predicted trajectory could then get their own benchmark entry and be evaluated against it.

Chapter 5
Are Biodiversity Measures suitable for assessing Restoration Success?

5.1. *Abstract*

The uncertainty about which ecosystem measures perform best for assessing restoration success remains unresolved. This issue is especially pressing for projects carried out in biodiversity offset settings, which have to predict when restoration success will be achieved. Species diversity indices are frequently employed to assess restoration success, despite the fact that they have received intensive critique over the last few decades and their suitability for this task is unclear. Other measures based on taxonomic and, especially, functional diversity have been suggested in preference to species based indices. Another option, frequently applied in restoration settings, focuses on specific species groups or functional types. The performance of all these different measures has rarely been tested in restoration projects. In this study, a range of widely used or suggested measures to evaluate (i) species, (ii) taxonomic, and (iii) functional diversity as well as (iv) functional group membership have been calculated over three forest successional sequences for the fern, shrub and tree tiers in a restoration project. Species diversity indices showed the strongest response over time and were easy to calculate and interpret, but provided a low information content regarding the status of the restoration project. Both, taxonomic and functional indices showed only weak to moderate trends over increasing successional time and were often correlated with species diversity measures. The clearest and easiest results to interpret, with the highest information content, arose from functional groups defined by dispersal mode, growth form, or successional type (e.g. late successional trees). It is suggested that these measures, together with other carefully chosen structural and compositional plant measures, are the best current choice for assessing development in restoration projects, especially if applied to biodiversity offset situations that require transparent and easy to interpret measures.

5.2. *Introduction*

The question of which ecosystem measures are most useful to assess long-term restoration success remains challenging. Attribute choice is especially difficult in biodiversity offset situations, as these require transparent and objective modelling and prediction of values to assess restoration success. Even though attribute selection depends on the specific project and its restoration goals, there are some measures which are commonly applied such as species diversity indices (Ruiz-Jaén & Aide 2005a). These indices are in general relatively easy to calculate, but their usefulness has been questioned (Buckland et al. 2005; Leinster & Cobbold 2012). Indices attempt to summarize complex processes in a single number, which can be difficult to interpret. An increase in diversity at one site can be misleading as it may be due to the colonisation of exotic or generalist species more adapted to the disturbed system, whilst specialist species are lost from the system (Catford et al. 2012; Mayor et al. 2015). Index results are also largely dependent on sampling effort and size (Magurran 2004). The whole matter is further complicated by the enormous range of indices to choose from (e.g. Chiarucci et al. 2011; Heip et al. 1998; Morris et al. 2014).

For restoration projects, species diversity has traditionally been viewed as a surrogate measure for ecosystem function and resilience: the more species present the more likely it is that some of them are redundant in terms of ecosystem function thus conferring greater resilience (Mori et al. 2013; Yachi & Loreau 1999). Some authors suggested that taxonomic or functional diversity indices might be better suited to investigate this feature (Cadotte et al. 2011; Desrochers & Anand 2004), and these have subsequently gained greater attention in ecological restoration in recent years (Laughlin 2014; Perring et al. 2015). Some conceptual issues have yet to be overcome, as the outcomes of functional diversity (FD) indices depend greatly on choice and number of traits used, and how they are weighted (Vellend et al. 2011), which in turn might depend on data availability. In practice, they are still rarely used and their application has been mostly limited to grassland restoration projects (e.g. Engst et al. 2016). As an alternative to functional indices, some restoration projects investigated the relative importance of certain functional groups, which are often defined by dispersal, growth form, or successional mode to assess restoration success (Lebrija-Trejos et al. 2010; Suganuma & Durigan 2015).

Taxonomic diversity indices (TD) have been suggested as surrogate measures for FD indices until the trait selection process has been further verified (Flynn et al.

2011). Taxonomic diversity views diversity from a different angle than species richness, focusing on the relatedness of taxa, and reasoning that closely related taxa might share similar traits (Desrochers & Anand 2004; Helmus et al. 2010). Species diversity might display a unimodal trend over a disturbance gradient (Bongers et al. 2009; Dornelas et al. 2011), whereas taxonomic indices may show a monotonic pattern with increasing disturbance as it has been suggested that these habitats hold species which are very closely related (Helmus et al. 2010; Tucker et al. 2016). The taxonomic indices introduced by Warwick and Clarke (K. R. Clarke & Warwick 2001; Warwick & Clarke 1995) were found to be independent of species richness and hence robust to sampling issues (Magurran 2005). They also have been shown to be sensitive to ecosystem degradation (Warwick & Clarke 1998). Unfortunately, their application has been mostly limited to aquatic ecosystems; for an exception see Moreno et al. (2009). As a result, the performance of these relatively new index groups has been rarely compared to the more traditional species based indices, especially for assessing restoration success.

This study addresses this shortfall and contrasts a range of the most commonly applied species, functional, and taxonomic indices as well as single measures of functional group membership across a restoration time-sequence at one study site. Attribute performance was tested in this case study with regard to (i) their ability to detect changes in ecosystem condition with increasing recovery time, (ii) their relationship with each other and hence their surrogate ability, and (iii) the information content when compared to a reference ecosystem.

5.3. *Methods*

5.3.1. Study Site and Research Design

See Chapter 3 pages 25 - 29 for a comprehensive description of the study site and the research design. Successional stages along the vegetation trajectories are described in Chapter 3 pp: 35 - 37.

5.3.2. Data Collection

A concentric, circular sampling plot design was chosen to account for the successional gradient ranging from early pioneer shrub to old growth forest. It represents a trade-off between keeping the sampling effort reasonable and still achieving the required accuracy. Three vegetation tiers were sampled: fern, shrub, and tree. In both the shrub and tree tier, all woody species present in that

layer were recorded. The shrub tier was defined as 0.5 - 3.5 m height and everything above this was assigned to the tree tier. For the ground layer only fern species were recorded due to the virtual absence of herbaceous plants. The fern layer was sampled within a 2 m radius circular plot and cover percentages for all fern species recorded. All woody species ≥1 cm dbh (dbh = diameter at breast height, 1.40 m) were counted within a 6 m radius plot and affiliation with the tree or shrub tier was noted. In the same plot, cover abundance (%) was estimated for each woody species under 3.5 m height. This was necessary to account for the shrub species, which were often found to be multi-leaders and difficult to count meaningfully, and are therefore better described by cover abundances. To account for the detection probability of larger tree sizes especially in the old growth forest, all tree species ≥ 20 cm dbh were recorded within a 12 m circular plot. In addition, all woody species present within the 12 m plot were recorded to establish an overall species list. The 6 m (plant height > 3.5 m) and 12 m plot data were then combined to create the tree tier data set. Comparison with the total species list indicated that species richness was slightly underestimated for the tree tier because of the area-species relationship (Magurran 2004). However, the objective was not to obtain an unbiased measure of species richness, which could be compared across studies, but rather to find a way to compare different index values across a successional trajectory. Vegetation tier cover was estimated by assigning modified Braun-Blanquet cover abundance scores within six cover classes (1 = < 1 %, 2 = 1 - 5 %, 3 = 6 - 25 %, 4 = 26 - 50 %, 5 = 51 - 75 %, 6 = 76 - 100 %) to each species (Hurst & Allen 2007). Height was measured with a Vertex 2 clinometer. At every sampling plot, several terrain characteristics were recorded including physiography, altitude, aspect, and slope.

5.3.3. Attributes Investigated

The analysis was carried out for all index groups separately and for each of the defined vegetation tiers. Functional groups were analysed using the woody plant dataset (6 m radius ≥ 1 cm in $d_{1.4}$). All analyses were carried out using R version 3.3.0 (R Core Team 2016).

Species Diversity

The most commonly used measures of species diversity were calculated: Shannon's (N_1) and Simpson's diversity (N_2), Simpson's evenness ($_qE$), and species richness (N_0). Instead of raw index numbers, converted values giving effective species numbers were used (Table 15). Effective species values provide

the theoretical number of species that would result in a certain index value in the case that all species contain the same number of individuals. These values are easier to interpret, especially between different indices, and provide a more stable and sensible measure of diversity (Hill 1973; Jost 2006). N_0 – N_2 represent three of Hill's diversity indices, giving decreasing weight to rare species. All three have been calculated to construct biodiversity profiles (Heip et al. 1998). For these profiles, the inherent dominance gradient between these indices is utilized. This means index values can be interpreted as providing the number of rarest species (N_0) to the most abundant ones (N_2) (Morris et al. 2014), whereas N_1 represents the true diversity, balancing both richness and evenness.

Simpson's evenness ($_qE$) was chosen because of its consistent response over an evenness gradient found in other studies and its insensitivity towards rare species (Smith & Wilson 1996). As all species diversity measures are notoriously sensitive to sample size and intensity, the quality and completeness of the sampling were investigated using species accumulation curves with exact and rarefied values. For the calculation of rarefied richness the function 'rarefy' was applied (based on Hurlbert, 1971) and subsample size was set to 50 individuals. There was a significant difference between species richness and rarefied richness (p<0.001) for all vegetation tiers. However, only 2% of variation was not explained between both variables (R^2 = 0.98, difference in species numbers: $mean_{tr}$ = 0.18, SE_{tr} = 0.03, $mean_{sh}$ = 0.28, SE_{sh} = 0.04, $mean_{fr}$ = 0.15, SE_{fr} = 0.02). Even though the bias introduced by joining different sized plots for the tree tier is likely to be higher than that, rarefied species richness is reported. For the calculation of these indices the 'BiodiversityR' (Kindt & Coe 2005) and 'Vegan' (Oksanen et al. 2016) packages have been used.

Taxonomic Diversity

Five levels of taxonomic classification (species, genus, family, order, class) were used, which were sourced from the New Zealand Plant Conservation Network (NZPCN 2016). Taxonomic trees used for calculating the taxonomic indices for the different vegetation tiers (i.e. tree, shrub, and fern) are given in Appendix 7. The following indices were chosen, as they specifically focus on identifying stress in ecosystems (K. R. Clarke & Warwick 2001; sensu K R Clarke & Warwick 1998; Warwick & Clarke 1995). These indices use the average taxonomic path length calculated between (1) two randomly chosen individuals (taxonomic diversity, Δ), (2) individuals drawn from different species (taxonomic distinctness, Δ^*) and (3) two randomly selected species (average taxonomic

distinctness (Δ^+). Δ and Δ^* both reduce to Δ^+ if only species presence/absence data is used. Δ^+ was employed for all species present in a sample as well as to build funnel plots via randomized subsampling (Δ^+ vs. number of species), as suggested by Warwick & Clarke (2001). Funnel plots use the overall species list of a region to create a 95 % probability funnel for Δ^+ values to be observed. Sampling plots outside these funnel limits will have significantly lower/higher Δ^+ values than expected, indicating a higher level of past disturbances or continuing anthropogenic stress. In addition, the evenness of taxa distribution across the hierarchical taxonomic tree (Λ^+) was computed, which also uses presence/absence data. All taxonomic indices were calculated with the function 'taxondive' from the Vegan package, using the recommended standard settings.

Functional Measures

Functional diversity (FD) can be explored either by applying some form of index or by considering selected functional groups in more detail. Both ways are investigated here.

Functional Indices

A set of plant traits was chosen to calculate FD indices thought to reflect plant adaptation and fitness to key life processes (e.g. seed dispersal) and possible barriers (e.g. fire, droughts, browsing) in Hinewai.

Reproduction potential was assessed by: *fruit size*, *type of seed dispersal*, and *mode of reproductive organs*. For an indication of plant total productivity and potential community dominance, *life mode / growth form (GF)* and *leaf mass per area* (LMA) were chosen. For resistance to potential stressors or disturbances that might be present in Hinewai, sensitivity to fire (i.e. *resprouting ability*), *palatability*, and *leaf width* (as a measure of drought resistance) were chosen. Life mode and leaf width were sourced from the Landcare Research ecological trait database (http://ecotraits.Landcareresearch.co.nz). Woody plants were categorized as belonging to the following growth forms: 'shrub', 'small tree' (3 -6 m), 'medium tree' (6 - 10 m) and the 'large tree' (> 10 m height) classification was further divided into 'early' and 'late' successional trees. Fruit type, size, and dispersal mode were obtained from Burrows (Burrows 1994a, 1994b). LMA(g/m^2) data were retrieved from the Landcare Research NZ datastore (Richardson et al. 2015). For more details of collection and preparation method see Mason et al. (2010). Functional diversity indices were only calculated for woody plants, singletons (i.e. species with only a single individual encountered across all

sample) were removed for this analysis. The focus has been on woody plants as they are the most dominant plant group in forests and therefore likely to have the greatest influence on ecosystem function and resilience.

The FD package (Laliberté et al. 2014) was used to calculate a range of widely used functional diversity indices. The package uses Principal Coordinates Analysis (PCoA) based on a species-by-trait matrix to create a multi-functional niche space (the hull), where each trait is represented by one PCoA axis. Functional diversity was then calculated by the distribution of communities across this functional space and their occupation within the hull (Villéger et al. 2008). Functional richness (FRic) reflects the total functional space filled by a community using presence/absence data. Functional evenness (FEve) depicts the uniformity of the trait abundance distribution within the functional hull. Functional divergence (FDiv) reflects the spread of trait abundances and the location of their clusters across this hull volume (Mason et al. 2005; Schleuter et al. 2010). In addition, functional dispersion (FDis), giving the mean distance of individual species to the centroid of all species in the community (Laliberté & Legendre 2010), and the related Rao's quadratic entropy (Q), providing the mean distance between species (Botta-Dukát 2005), were calculated. Finally, functional group richness (FGR), giving the number of functional groups present in a community (Petchey & Gaston 2006), was computed. Woody species were classified into functional groups by hierarchical clustering using a Euclidean trait distance matrix as input. The functional dendrogram was cut by setting it to a total of eight groups for the shrub tier and to seven for the shrub layer (see Appendix 8 for functional dendrograms used). Aside from applying the 'Cailliez' correction for matrices, which could not be displayed in Euclidean space, standard settings were used and no weighting was applied. For calculation details see the FD package and references listed in Table 16.

Functional Group Measures

All traits were also investigated individually for the dbh ≥ 1 cm (6 m radius plot), to identify any trends over time. This was not done separately for each tier so that shrub and tree species could be included together. However, only groups where significant changes occurred over time are discussed further. These groups are growth form (GF) and dispersal mode (as described on page 79).

Table 15. Overview of all species and taxonomic indices used in this research.

Index	*Formula*	*Range*	*Reference*
Shannon diversity	$N_1 = \exp(-\sum p_i \ln p_i)$	[0, ∞]	Hill(1973), Jost (2006), Shannon(1948)
inverse Simpson diversity	$N_2 = 1/(\sum_{i=1}^{S} p_i^2)$	[1, ∞]	Hill(1973), Simpson (1949), Hurlbert (1971)
Simpson's evenness	${}^{q}E = N_2/ N_0$	[0, 1]	Smith & Wilson (1996), Tuomisto(2012)
Species richness (H_0)	N_0 = number of species	[0, ∞]	
Average tax. diversity	$\Delta = \frac{\sum\sum_{i<j} w_{ij} x_i x_j}{N(N-1)/2}$	[0,100]	Warwick & Clarke (1995)
Taxonomic distinctness	$\Delta^* = \frac{\sum\sum_{i<j} w_{ij} x_i x_j}{\sum\sum_{i<j} x_i x_j}$	[0,100]	Warwick & Clarke (1995)
Variation in tax. distinctness	$\Lambda^+ = \frac{\sum\sum_{i<j} (w_{ij} - \Delta^+)^2}{S(S-1)/2}$	[0,1000]	Clarke & Warwick (2001)
Average tax. distinctness	$\Delta^+ = \frac{\sum\sum_{i<j} w_{ij}}{S(S-1)/2}$	[0,100]	Clarke & Warwick (1998)

For the species diversity indices, p_i is giving the proportion of all individuals for species i to all individuals in the sample. For the taxonomic indices ω_{ij} denotes the taxonomic path length between

Table 16. All functional indices investigated in this research, for calculation details see references given.

Functional diversity indices	*A*bbrev.	*Range*	*References*
Functional dispersion	FDis	[0 , ∞]	Laliberté & Legendre (2010)
Functional divergence	FDiv	[0 ,1]	Villéger et al.(2008)
Functional evenness	FEv	[0 ,1]	Villéger et al.(2008)
Posteriori functional group richness	FGR	[0 ,$7_{tr}(8_{sh})$]*	Petchey & Gaston (2006)
Rao's quadratic entropy	Q	[0 , ∞]	Botta-Dukát (2005)
Functional richness	FRic	[0 , ∞]	Villéger et al.(2008)

**Upper limit is given for this study.*

5.3.4. Statistical Analysis

Both broadleaved trajectories are structurally very similar, it was therefore investigated if an individual analysis could be justified. Permutational Multivariate Analysis of Variance (PERMANOVA) using the Adonis function from the Vegan package was carried out. All attributes were standardized beforehand and Euclidean distances were used to calculate the distance matrix; recovery time was included as a covariate to correct for differences in observation time between successional stages. Adonis requires the homogeneity of dispersion among groups, which can be tested by using the betadisper function in conjunction with a permutation test (function permutes). The groups showed no significant difference in dispersion (variances) ($p > 0.05$, $nPr = 99$). A significant difference between both successional stage means was obtained ($F(1,74) = 4.34$, partial $R^2 = 0.05$, $p > 0.01$, $nPr = 99$), hence both trajectories were analysed as two distinct trajectories.

To test if there was an association between time of abandonment and attribute development, all attributes were subjected to Spearman's rank-order correlation (r_s) test. This non-parametric test was chosen as it is robust to non-normal data and non-linear relationships between variables and outliers (Zuur et al. 2007). This test uses ranks and therefore no data standardisation is required. P-values were corrected for multiple comparisons using Holm's method (Holm 1979). Relationships of attributes that had a significant association ($p < 0.05$) with time were further investigated using standard linear regression methods. Diagnostic plots were used to verify the underlying assumptions of homogeneity of variance and normality of residuals to assess model fit. Data transformations such as log or logit were applied when needed to fulfil model assumptions. The main objective was not to find the perfect model, but rather to find a curve that approximates the underlying relationship between recovery age and the ecosystem attribute.

Finally, a correlation analysis using Pearson's r (r_p) for each attribute with recovery time was carried out individually using, when required, the transformed data from the regression analysis. Pearson's r was used, as it readily translates into R^2. Correlation results were calculated and plotted using packages corrplot (Wei 2013) and psych (Revelle 2015).

To get an indication of attribute development stage and differences in final indices results (uppermost end of age range), values were compared between

each trajectory as well as to reference forest values. Information content and ease of interpretability for the different indices were assessed. When time had a significant effect on attribute values ($p < 0.05$), the last modelled data point was used (highest plot age). When no significant trend was apparent, the mean values of the attribute were used over all sampling plots.

5.4. *Results*

5.4.1. Attribute Relationship with Recovery Time

Pearson's correlation results (corrected according to regression analysis) for all attributes tested are shown in Figure 14, with attributes which did not display a significant trend over time ($p > 0.05$) left blank.

Species Diversity
Attribute correlation strength over time for the species indices largely reflected the relative importance of a tier (e.g. tree, shrub or fern cover abundance) in the ecosystem (Table 17).

Table 17. Summary of study site characteristics, providing number of sampling plots in each forest trajectory (across all associated successional stages) and the reference forest. The successional time frames covered, as well as mean cover percentages of each vegetation tier at the start and end of the observation time frames are given. Māhoe and fuchsia trajectories share 27 plots in the earlier successional stages (pasture, gorse, and emergent natives), after which both trajectories diverge. Control plots are located outside of Hinewai Reserve in directly adjacent farmland.

Vegetation trajectory / type	Number of plots		Age range (years)	Fern tier (mean ±SD)		Shrub tier 0.5 -3.5m (mean ±SD)		Tree tier > 3.5m (mean ±SD)		
	Hinewai	Control		Cover start (%)	Cover end (%)	Cover start (%)	Cover end (%)	Cover start (%)	Cover end (%)	height (m)
Kānuka	33	10	20-120	6.7 ±5.1	24.4 ±20.5	12.9 ±9.4	61.7 ±4.9	83.8 ±13.4	57.7 ±17.7	12.4 ±0.9
Māhoe	38	1	15-70	8.3 ±12.9	21.7 ±20.1	92.1 ±35.1	53.3 ±35.1	8.9 ±7.1	87.9 ±10.3	5.5 ±1.8
Fuchsia	42	6	15-87	8.3 ±12.9	40.6 ±25.3	92.1 ±25.0	43.1 ±25.0	8.9 ±7.1	87.1 ±19.2	6.5 ±1.4
Old growth	17	5	>100	37.8 ±24.7	-	30.9 ±19.5	-	79.1 ±8.6	-	30.9 ±19.3
Total	105	22								

The kānuka trajectory displayed the strongest trends in species diversity for the tree and shrub tier, whereas all fern tier index results were non-significant ($p > 0.05$). In both broadleaved trajectories, tree tier related changes over time were most pronounced. While trend strength was similar across the shrub and fern tier for māhoe (weak = $r_p < 0.5$ to medium= $r_p > 0.5$), the fern layer showed an overall stronger correlation with time (medium-strong = $r_p > 0.75$) than the shrub layer in the fuchsia forests (weak - medium). Most measures of species diversity displayed a logarithmic response shape over time while some had a linear

relationship (kānuka) (Figure 13). Species richness showed the strongest correlation with recovery time within the species diversity indices (Figure 14). Simpson's evenness (^{q}E) displayed a negative trend with time over all vegetation tiers and trajectories.

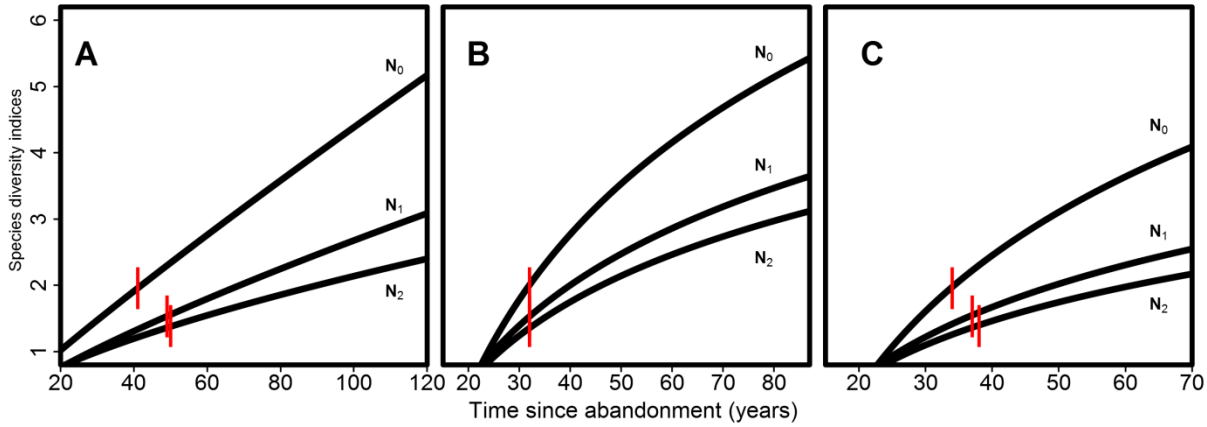


Figure 13. Development of species richness (N_0), Shannon's (N_1) and Simpson's index (N_2) over increasing recovery time in the tree tier ; modelled with standard regression methods. For (A) kānuka (N_0, R^2 =0.50***; N_1, R^2=0.50*** N_2 ; R^2 = 0.38***), (B) fuchsia (N_0, R^2=0.57***; N_1, R^2=0.52***;N_2, R^2 = 0.50***) and (C) māhoe (N_0, R^2=0.56***; N_1, R^2=0.14*; N_2, R^2=0.06^{ns}), the mean value for the reference (red beech forest) is represented by a red bar. Statistical significance is indicated by: ns (non-significant) =p > 0.05, *=p ≤ 0.05, **=p ≤ 0.01, ***=p ≤ 0.001.

Taxonomic Diversity

For the taxonomic diversity indices no strong correlation (r_p > 0.75) with increasing recovery time was found. The variation in taxonomic distinctness (Λ^+) produced the most consistent weak (r_p < 0.5, p < 0.05) to medium (r_p > 0.5, $p \leq$ 0.01) positive trend for all trajectories within the tree and fern layer, but was not significant for the shrub tier (p > 0.05). This finding indicates that species were becoming more taxonomically distinct in the tree and fern tier over time.

Functional Measures

Dispersal and growth form displayed a strong correlation with recovery time. Dispersal mode showed a strong trend over time from gravity (r_p > -0.75) to bird dominated (r_p > 0.75) in both broadleaved trajectories, and a weaker shift from wind dispersed (r_p > -0.50) to bird distributed in kānuka (r_p > 0.50). This trend reflects the decreasing dominance of gorse (gravity dispersed) and kānuka (wind dispersed), which coincides with an increase of broadleaved species that are commonly bird-dispersed in these forests. The percentage of shrubs also decreased over time, favouring a higher proportion of medium sized trees (6 - 10 m height) in the broadleaved trajectories. Larger pioneer trees (e.g. kānuka) retreated (r_p > -0.50) with progressing successional time in the kānuka forest.

Of all functional diversity (FD) indices, only functional group richness (FGR) displayed a significant weak to strong response across tiers and forest types. Kānuka displays weak to strong trends in almost all indices and for both tiers, probably caused by the increasing dominance of broadleaved species and the decline of kānuka. The correlations are less prominent in fuchsia and here only obvious in the tree tier. Māhoe shows the lowest response in functional diversity indices over time especially in the tree tier (Figure 14). The quality of functional richness (FRic) and functional dispersion (FDis) presentation, which might be compromised by using only a subset of principal coordinate analysis (PCoA) axes, can be inspected by an R^2-like ratio. The value was rather high for the tree tier (0.56) and relatively low for the shrub tier (0.37) (for more details see (Laliberté & Legendre 2010; Legendre & Legendre 1998). The strength and kind of attribute correlation with time varied widely between all trajectories. Species diversity measures possess a stronger correlation with recovery time than either taxonomic or functional indices.

5.4.2. Relationship between Ecosystem Attributes

Three correlograms (Figure 16) were used to investigate relationship consistency within and between different attribute groups for each trajectory. A correlation does not imply causality. If two attributes seem to be strongly correlated, it might be that both are actually correlated with recovery time instead of each other (cross-correlation). On the other hand, if two attributes show a correlation, but do not show this with increasing recovery time, it might be an indication that a correlation exists.

Species Diversity

Within the species diversity measures, species richness, Shannon's index, and Simpson's index showed their well-known correlation in all trajectories and vegetation tiers. Correlation between N_1 and N_2 was always higher than their correlation with recovery time, for species richness this was only found in 45% of index results. Simpson's evenness was in all cases negatively correlated with species richness and in all but one case significantly correlated with time (fuchsia/shrub tier $r_s = -0.12$, $p > 0.05$).

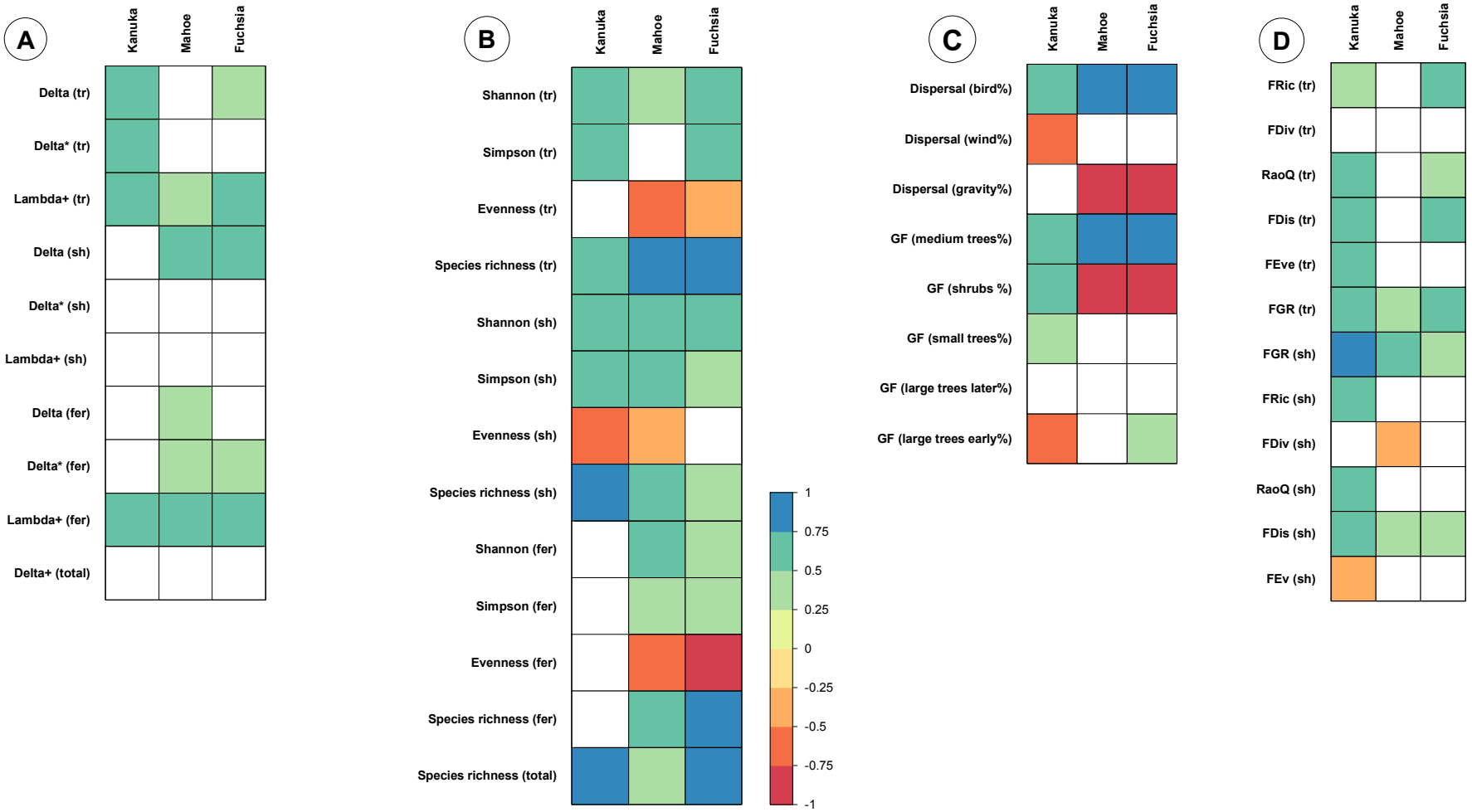


Figure 14. Results of correlation analysis (Pearson's *r*) on appropriate transformed data for ecosystem attribute development over progressing recovery time. Non-significant correlation results ($p > 0.05$) are left blank. Taxonomic diversity (A), species diversity (B), functional group measures (C) and functional indices (D) are shown separately.

Taxonomic Indices

Trends found in species measures were either only weakly reflected in average taxonomic diversity (Δ) (i.e. ferns showing a stronger trend in the broadleaved trajectories than in kānuka) or showed a different trend (no or negative trend in the shrub layer in kānuka) in the taxonomic indices. Over all trajectories and vegetation tiers, a higher correlation with Shannon's/Simpson's indices was observed than with recovery time. The response shape over time to ecosystem recovery in Δ was similar to the one shown by the species diversity indices for the kānuka and fuchsia forest (Figure 15). There was no apparent clear trend for the māhoe forest. The relationship between the species indices and taxonomic distinctness (Δ^*) was less obvious. Even though a significant correlation between species indices and Δ^* was observed in 45 % of all results this might be a result of cross-correlation, as only 27 % were not more strongly correlated with recovery time (as explained above). Variation in taxonomic distinctness (Λ^+) was more strongly correlated with species indices than with time in 45 % of all cases, interestingly it was most strongly confounded with the Shannon index. It was also found to be negatively correlated with Simpson's evenness (54 %), but this could be a result of cross-correlation with recovery time as in only 9 % was more strongly correlated with evenness than with time. Taxonomic distinctness (Λ^+) was also found to be either positively (species richness, diversity) or negatively related (evenness) with species diversity indices.

Functional Measures

FDis showed in only 50 % of the results (3 out of 6 cases) a significant trend over time and was often more strongly correlated with species richness (83 %). For all functional indices, inconsistent correlations with taxonomic indices were observed. Rao's quadratic entropy and FDis also showed in all cases a strong correlation ($rs > 0.75$), which has been already noted elsewhere (Laliberté & Legendre 2010). All functional indices were also found to be highly correlated with species diversity measures.

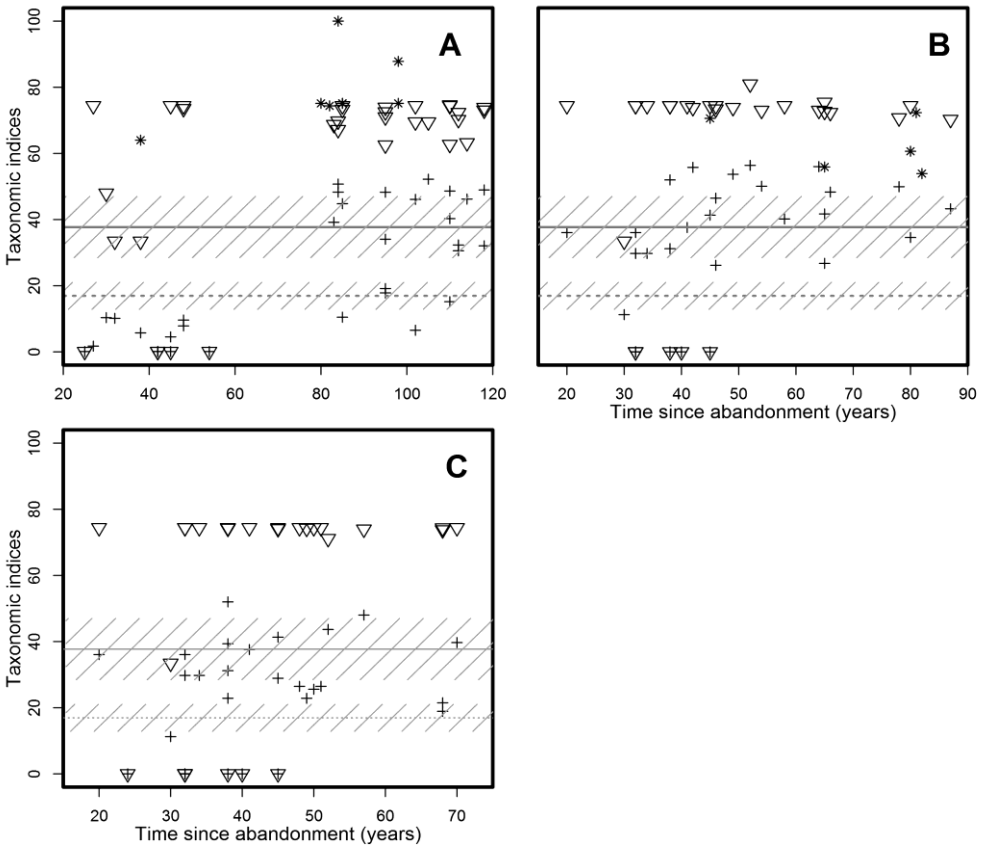
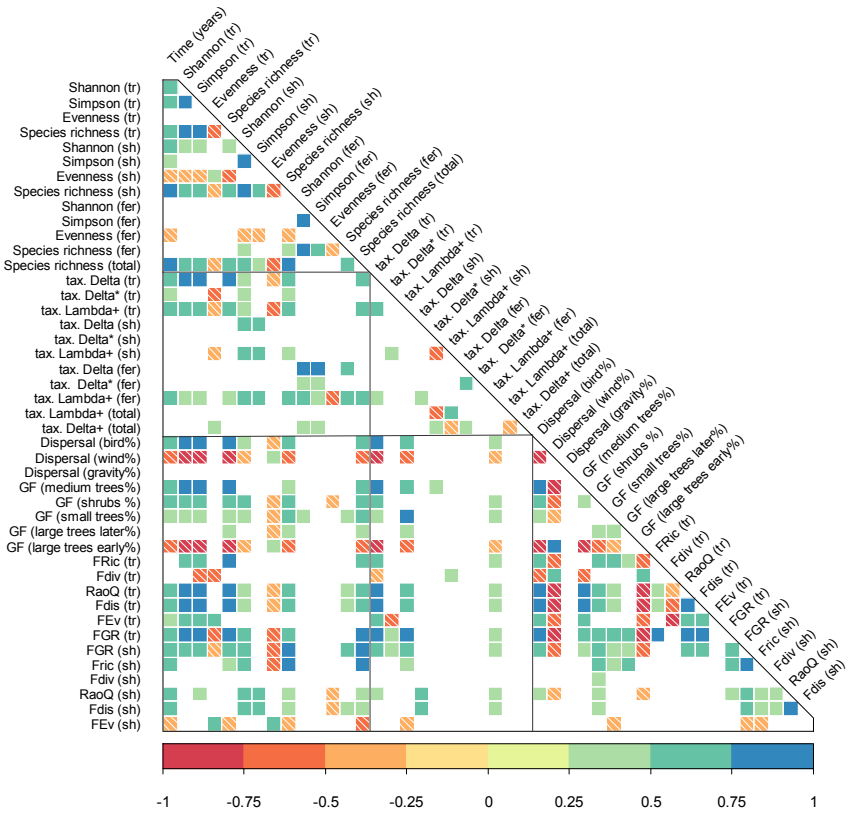
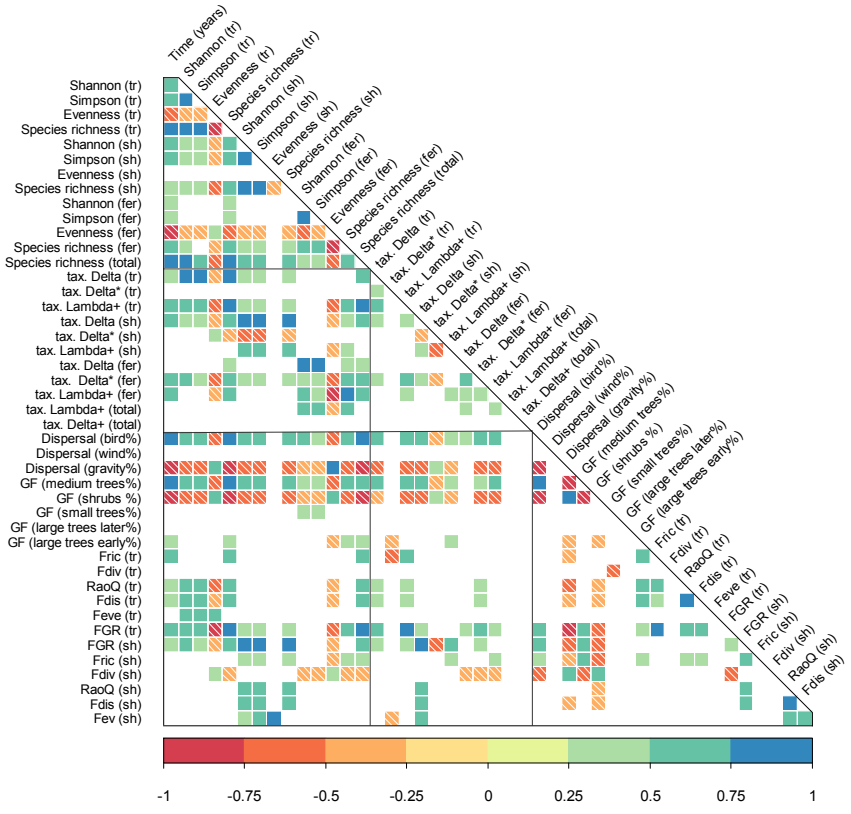


Figure 15. Taxonomic index results for individual sampling plots are displayed over estimated plot age. Values for Δ (cross) and Δ* (triangle) are given for the tree tier for (A) kānuka, (B) fuchsia, (C) māhoe within Hinewai Reserve. Stars (Δ*) are representing still grazed plots, outside of Hinewai. The shaded area and lines are indicating reference forest values. The dotted line represents mean Δ, the solid line depicts Δ* and the shaded area is respectively giving the SE of the mean.

A


Time (years)
Shannon (tr)
Simpson (tr)
Evenness (tr)
Species richness (tr)
Shannon (sh)
Simpson (sh)
Evenness (sh)
Species richness (sh)
Shannon (fer)
Simpson (fer)
Evenness (fer)
Species richness (fer)
Species richness (total)
tax. Delta (tr)
tax. Delta* (tr)
tax. Lambda+ (tr)
tax. Delta (sh)
tax. Delta* (sh)
tax. Lambda+ (sh)
tax. Delta (fer)
tax. Delta* (fer)
tax. Lambda+ (fer)
tax. Lambda+ (total)
tax. Delta+ (total)
Dispersal (bird%)
Dispersal (wind%)
Dispersal (gravity%)
GF (medium trees%)
GF (shrubs %)
GF (small trees%)
GF (large trees later%)
GF (large trees early%)
FRic (tr)
Fdiv (tr)
RaoQ (tr)
Fdis (tr)
FEv (tr)
FGR (tr)
FGR (sh)
Fric (sh)
Fdiv (sh)
RaoQ (sh)
Fdis (sh)
FEv (sh)
-1
-0.75
-0.5
-0.25
0
0.25
0.5
0.75
1

B


Time (years)
Shannon (tr)
Simpson (tr)
Evenness (tr)
Species richness (tr)
Shannon (sh)
Simpson (sh)
Evenness (sh)
Species richness (sh)
Shannon (fer)
Simpson (fer)
Evenness (fer)
Species richness (fer)
Species richness (total)
tax. Delta (tr)
tax. Delta* (tr)
tax. Lambda+ (tr)
tax. Delta (sh)
tax. Delta* (sh)
tax. Lambda+ (sh)
tax. Delta (fer)
tax. Delta* (fer)
tax. Lambda+ (fer)
tax. Lambda+ (total)
tax. Delta+ (total)
Dispersal (bird%)
Dispersal (wind%)
Dispersal (gravity%)
GF (medium trees%)
GF (shrubs %)
GF (small trees%)
GF (large trees later%)
GF (large trees early%)
Fric (tr)
Fdiv (tr)
RaoQ (tr)
Fdis (tr)
Feve (tr)
FGR (tr)
FGR (sh)
Fric (sh)
Fdiv (sh)
RaoQ (sh)
Fdis (sh)
Fev (sh)
-1
-0.75
-0.5
-0.25
0
0.25
0.5
0.75
1

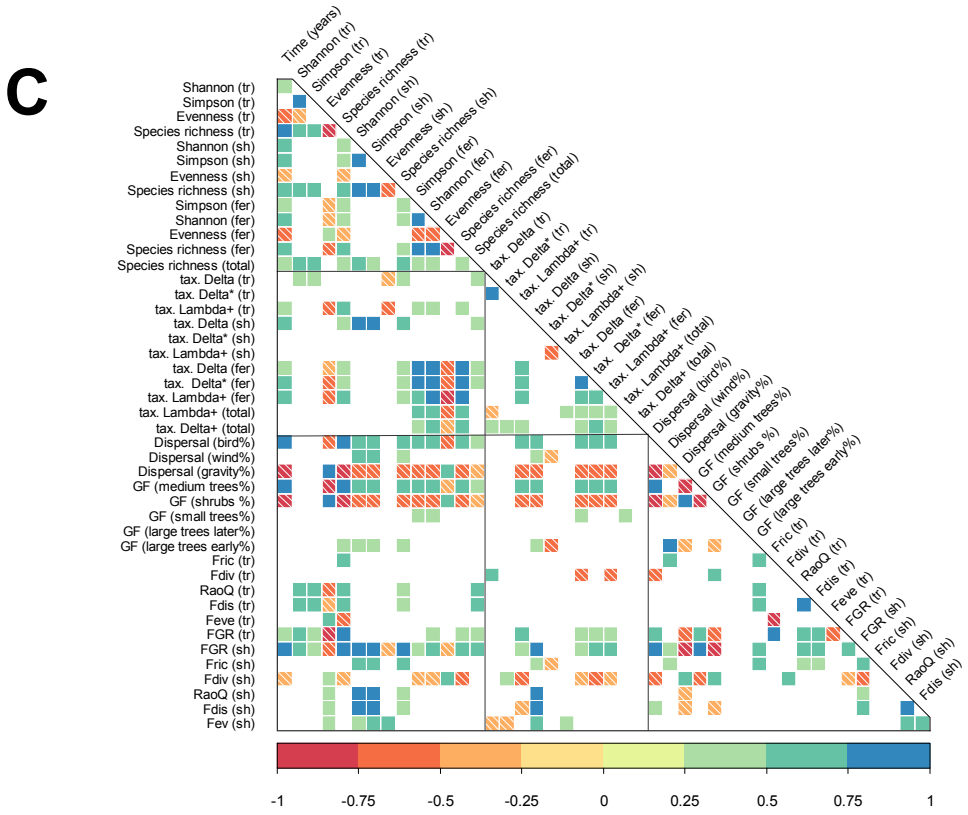


Figure 16. Correlation matrix plots of all tested biodiversity measures for the kānuka (A), fuchsia (B) and māhoe (C) trajectory. Colours reflect the strength and direction of Spearman's rank correlation, (e.g. blue = strong positive, red = strong negative). Non-significant results are left blank ($p > 0.05$). Findings are given for all three vegetation tiers: fern (fer), shrub (sh) and tree (tr).

GF = growth mode, Fric – Fev denote functional diversity indices, see Table 16 for an explanation of abbreviations used.

5.4.3. Attribute Convergence towards the Reference

Regression results or mean values for all attributes were inspected either for the highest development age or across all plots, depending upon whether a significant relationship ($p < 0.05$) with recovery time existed. This was undertaken respectively for each diversity group and reference forest values are provided for comparison (Figure 18 + 19). These results should be viewed with caution as model R^2 was often below 0.50 and, as already stated, means across all plots were frequently used. Not too much weight should be therefore given to the absolute values; the focus should lie on the relative differences among forest types. Attribute values are examined in more detail for the tree tier (being the most dominant in the forest) (Figure: 13, 15, 17, and 20).

Species Diversity

A total of 21 species were found in the tree layer, 37 species were present in the shrub tier, and 21 ferns were identified over all stages and trajectories. Model

results suggested that tree tier reference values were reached early on in the two broadleaved trajectories (32 - 38 years), whereas kānuka took a few years longer (41 - 50 years). Species richness values converged first for all forest types. Observed values in the māhoe forest after 70 years of recovery were reached 10 - 20 years earlier in the fuchsia dominated forest (Figure 13). Diversity profiles were examined at two points in time for the tree tier, after 30 years of recovery and at the end of the observation time using the slope between different order indices (Figure 17). If the last point in time is examined, kānuka shows the highest degree of dominance (slope = -1.38), followed by fuchsia (slope = -1.154) and māhoe being the most even one (slope = -0.959). However, the same results are given by Simpson's evenness index: kānuka (^{q}E = 0.58, SE = 0.04), fuchsia (^{q}E = 0.53, SE = 0.13), and māhoe (^{q}E = 0.40, SE = 0.19). Interestingly, beech shows the highest degree of evenness (slope = -0.28), which can only be explained by the small number of species present in the tree layer ($N_{0,}$ mean=1.95, SE=0.26). Shifts in relative distances between indices over time seem to indicate that evenness in all communities was initially high (Figure 17) but decreased over time. Contrary to this, Simpson's evenness (trees) did not show a significant trend over time for kānuka. However, a maximum of two species were present in all successional trajectories within the first 30 years of recovery. Both diversity profiles as well as Simpson's evenness seem to indicate high evenness in the presence of very few species. As expected, the shrub layer included more species in all forest types (including the reference forest) than the tree tier, as a result of combining shrub and tree species. Kānuka reaches the highest values for all measures, probably reflecting the transition into the next development stage. Ferns showed no trends in the kānuka trajectory, which is not surprising as the general cover percentage was much lower than in the broadleaved forest (Table 16). In contrast, the fern layer within the broadleaved forest became more diverse over time. All second growth forests held more fern species than the reference site and broadleaved trajectories also displayed a higher evenness. All species diversity indices showed a consistent trend over time and behaved in a similar way (e.g. Figure 13).

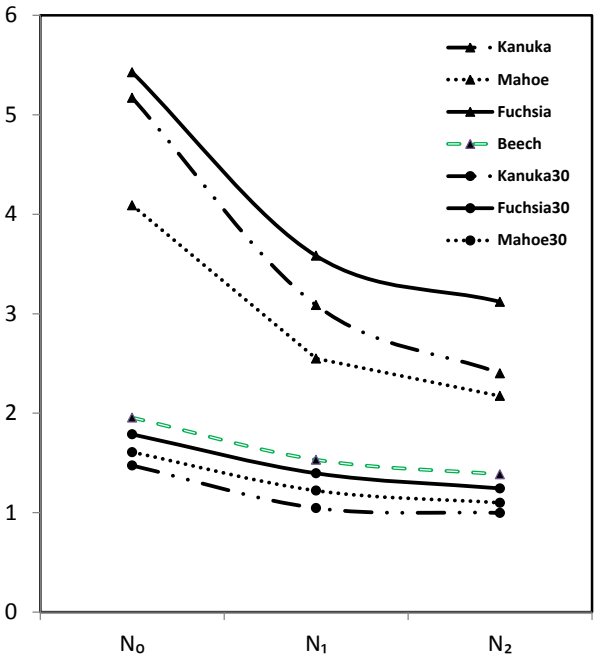


Figure 17. Species diversity profile for all forest trajectories and the reference forest. Species diversity indices giving decreasing weight to rare species are employed, N_0 = species richness, N_1 = Shannon's index, N_2 = Simpson's index. Modelled values are shown for the last available point in time and after 30 years of recovery.

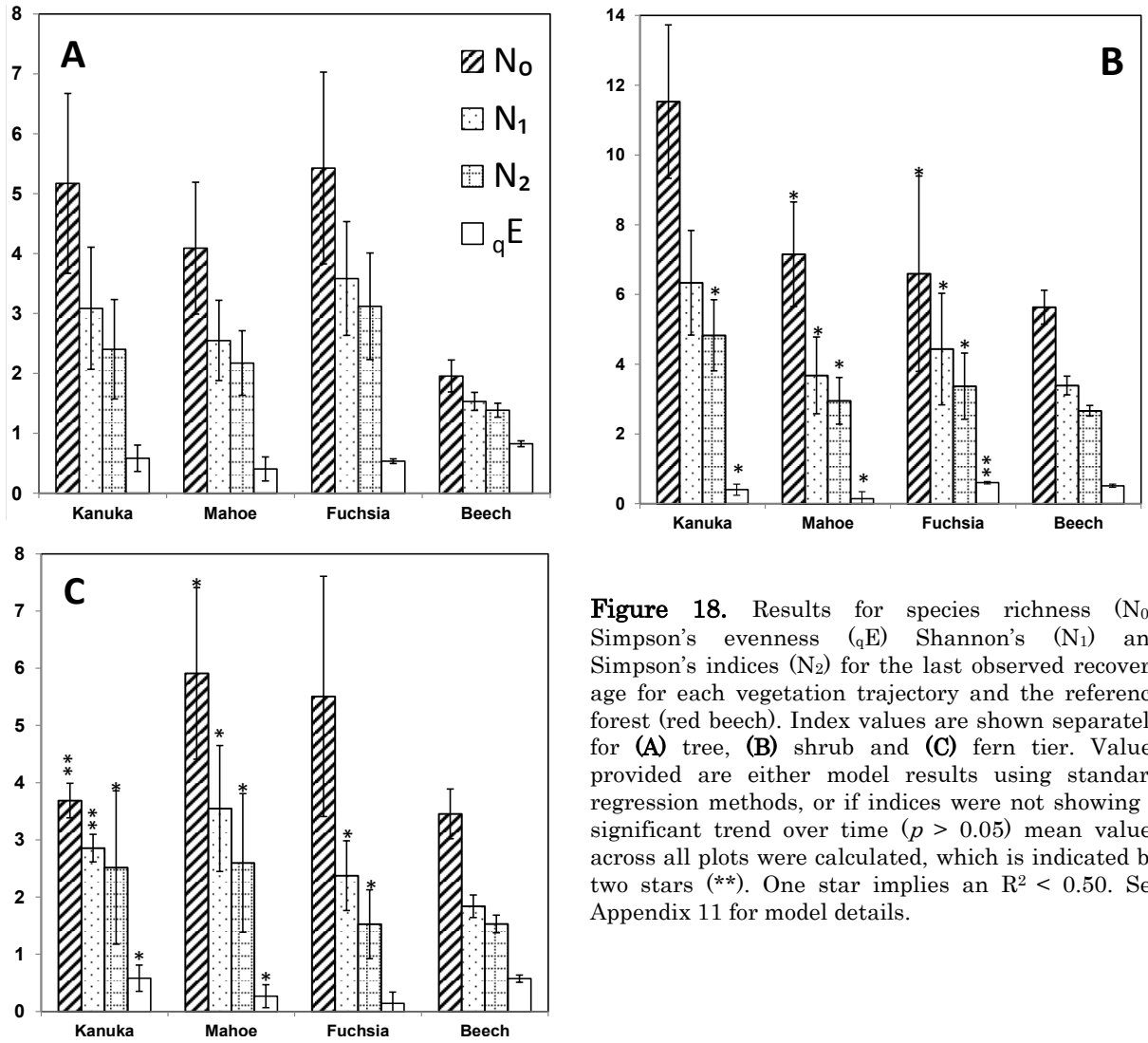


Figure 18. Results for species richness (N_0), Simpson's evenness ($_qE$) Shannon's (N_1) and Simpson's indices (N_2) for the last observed recovery age for each vegetation trajectory and the reference forest (red beech). Index values are shown separately for **(A)** tree, **(B)** shrub and **(C)** fern tier. Values provided are either model results using standard regression methods, or if indices were not showing a significant trend over time ($p > 0.05$) mean values across all plots were calculated, which is indicated by two stars (**). One star implies an $R^2 < 0.50$. See Appendix 11 for model details.

Taxonomic Diversity

Index results are depicted over time only as sample plot values without a trend line (regression line) for comparability over all forest types (Figure 15 for tree tier and Appendix 10 for shrub tier). This was necessary, as the effect of recovery time on these indices was generally low ($R^2 < 0.045$ / $r_p < 0.67$) and often not significant (see Figure 14, or Appendix 11 for model details).

Values of Δ range between 0 and 100, zero implies that all individuals belong to the same species and 100 denotes the longest possible distance, meaning all individuals residing in the same proportions in different taxonomic orders. Response shape over recovery time was similar (Figure 15, Appendix 10), but more diffuse than the results shown by the species diversity indices for the kānuka and fuchsia forest (Figure 13). No clear trend was apparent for the māhoe forest. Mean Δ_{tr} for the reference forest was very low (Δ_{tr} = 16.94, SE = 4.08), it was highest in fuchsia forest (Δ_{tr} = 53.75, SE = 8.93, $p < 0.001$), followed by kānuka (Δ_{tr} = 47.99, SE = 8.17, $p < 0.001$), and low without showing a trend over time in māhoe (Δ_{tr} = 24.79, SE = 3.11). Reference values for the tree tier were reached in less than 40 years in fuchsia, whereas kānuka needed over 60 years. The effect of the underlying species abundance distribution, which seems to heavily influence Δ, is removed by using Δ^*, where delta is divided by the values of the Simpson index. Δ^* is regarded as a true measure of taxonomic diversity. Again Δ^* is rather low for beech (Δ_{tr}^* = 37.72) and shows a large variation (SE = 9.27), probably reflecting that even the reference system is not undisturbed and was frequently harvested and burned in the past. All trajectories produce similar mean values for Δ^* at the end of the observation period (Δ^* = 71 - 75) (Figure 19). Disturbed systems are expected to show a decreased Δ^* value when compared with their normal range. Therefore, lower values are expected at the beginning of the successional development or in plots where some level of anthropogenic induced stress remains present in the system. The described behaviour was not very pronounced for the vegetation trajectories in Hinewai. A few younger sampling plots showed the described pattern, others did not (Figure 15). Some of the sampling plots outside of Hinewai (i.e. being still grazed), show lower or higher Δ_{tr}^*values as comparable vegetation plots in Hinewai. The shrub tier showed similar trends, but values for the reference were higher for mean Δ_{sh}^* (82.83) than for the three forest trajectories (Appendix 10). Reference values for Δ_{tr} were reached in all forests after about 40 years (Figure 15). Index results for the fern layer displayed, especially for Δ^*_{fer}, a high variation (Δ^*_{fer}= 30 – 100) between plots, across all trajectories and the reference side.

Taxonomic distinctness (Λ^+) was highest for the fern layer and lowest in the tree tier. Only within the shrub tier, the reference forest outperformed the secondary forests, suggesting that species were more taxonomically distinct. Constructed funnel plots (Δ^+ vs. number of species) for each tier, including all sampling plots in and outside of Hinewai, singled out individual plots (see Appendix 12). These plots are supposed to have experienced a higher level of disturbance than the other ones (Warwick & Clarke (2001). However, after individual inspection of these sampling plots no obvious reason for this classification could be found.

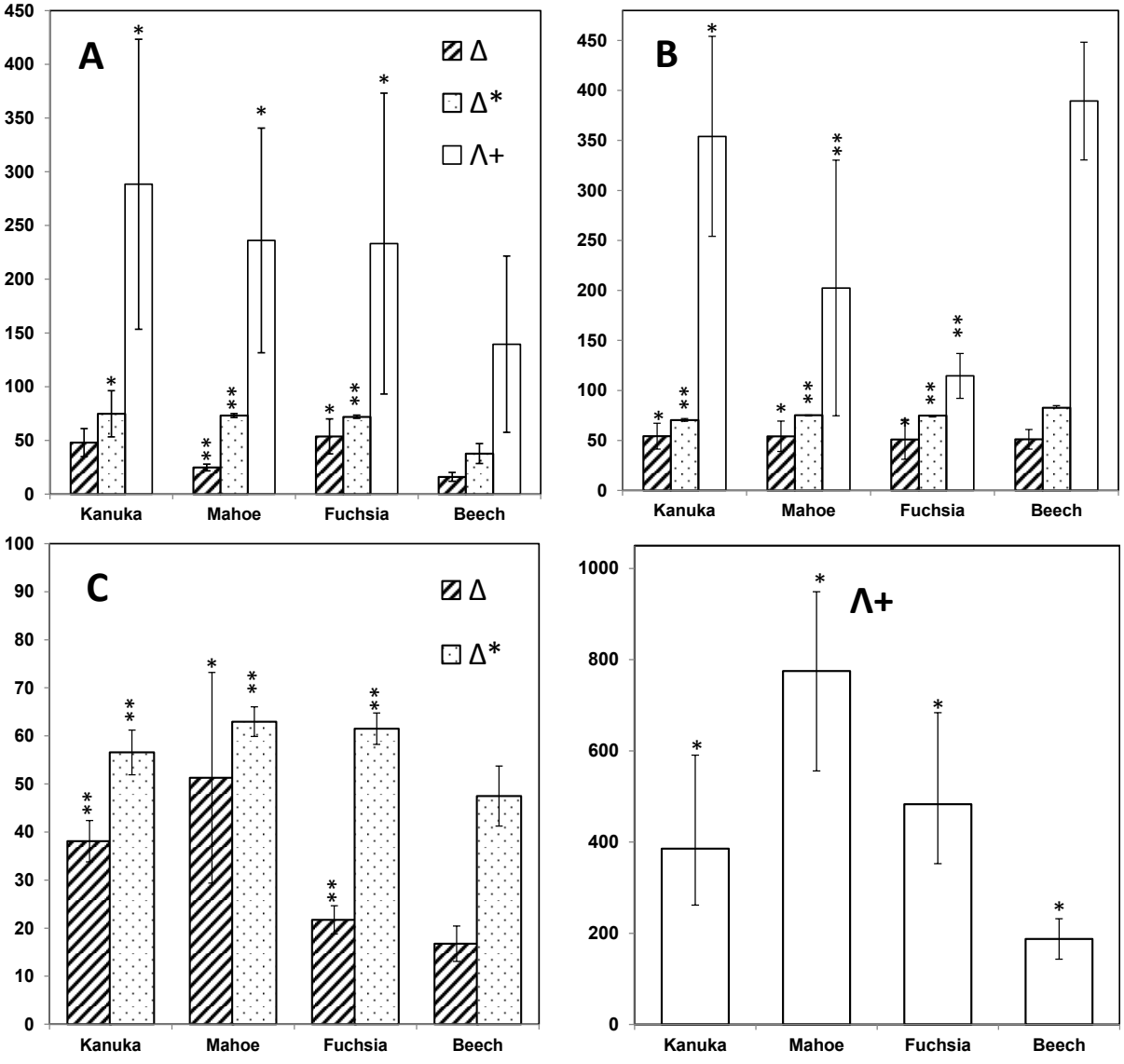


Figure 19. Index results for average taxonomic diversity (Δ), taxonomic distinctness (Δ*) and variation in taxonomic distinctness (Λ+) for the tree tier are shown in **(A)**, shrub layer in **(B)** and fern tier in **(C)** and **(D)**. Values are given for the latest observed plot age for each vegetation trajectory and the reference forest. Values provided are either mean model results (±SE) using standard regression methods or if indices were not showing a significant trend over time ($p > 0.05$) mean (± SE) values across all plots were calculated, which is indicated by two stars (**). One star implies an $R^2 < 0.50$. See Appendix 11 for regression model results.

Functional Measures

Results of modelled trajectory end values (last observation point in time) are provided in Table 18. Attributes that did not show a significant trend over recovery time were averaged across all sampling plots within a vegetation trajectory. Even for attributes that showed a significant trend over time, the coefficient of determination was often low (Appendix 11, Figure 14). Therefore, results need to be treated with extreme caution.

Functional Groups

As expected, most woody plants within the reference forest belonged to the group of later successional tree species (89 %) (Table 18). Trees of this group were extremely rare in all three second growth forests. The oldest mixed-broadleaved forests held the highest proportion of medium-sized trees, whereas in the oldest kānuka forest the earlier successional large trees (e.g. kānuka) were still most abundant. The high proportion of red beech in the reference forest was reflected by a high wind dispersal rate for woody species. All woody species within the oldest mixed-broadleaved forest types (māhoe and fuchsia) are mainly bird-dispersed, with the oldest kānuka forest still possessing a high wind dispersal rate (reflecting kānuka presence). Gorse is the major species in the group of woody plants that are dispersed by gravity in this data set; the low values displayed are caused by the absence of this light demanding pioneer species in later successional stages (Table 18).

Functional Indices

In both woody vegetation tiers the largest number of functional groups were present in kānuka (FGR_{tr} = 4.32, SE = 0.01; FGR_{sh} = 6.97, SE = 0.40). In the tree tier the fewest were present in the reference forest (FGR_{tr} = 1.82, SE = 0.24). The difference in FG group numbers is less obvious for the māhoe, fuchsia and beech forests in the shrub tier. To further investigate patterns within functional groups a non-metric multidimensional scaling ordination (NMDS) was carried out for each vegetation tier. The NMDS showed a distinct pattern for functional groups present in the tree tier in the different successional stages of the forest trajectories, but a pattern was less distinct for the shrub tier (Appendix 13). This is reflected by the weak differences between shrub tier values for all forest types. For the māhoe trajectory only a limited number of indices were significantly correlated with recovery time, from which only FGR (shrubs) showed a medium trend (r_p = 0.69, $p < 0.001$). The māhoe forest will therefore not be further considered.

Functional richness (FRic), which was measured as minimum convex hull volume, was largest in the kānuka forest. FRic does not incorporate species abundances. Rare species might therefore inflate the hull volume. Functional dispersion (Rao's Q, FDis) includes species abundances, placing more weight on dominant species and might therefore be a better measure of functional diversity. FDis provides the average distance of individual species to the centroid of all species. Both indices vary slightly in their calculation but have been found to be highly correlated (Laliberté & Legendre 2010). For the tree tier, FRic as well as Rao's Q and FDis were ranking the forest types consistently, from kānuka, to fuchsia, to beech forest that held the lowest values (Table 18)
). However, the differences between the forest types are at a larger magnitude if Rao's Q is inspected, and less distinct in FDis. This might be caused by FDis being less sensitive to extreme values than Rao's Q (Lalibert 2011).

All indices displayed a large variation within the sampling plots results, which impeded interpretation (e.g. Figure 20). Still, results indicate that reference values for $FDis_{tr}$ are reached relatively early on (Figure 20). Functional divergence (FDiv) did not change significantly over time in the trajectories (except a weak negative correlation for the māhoe – shrub tier).

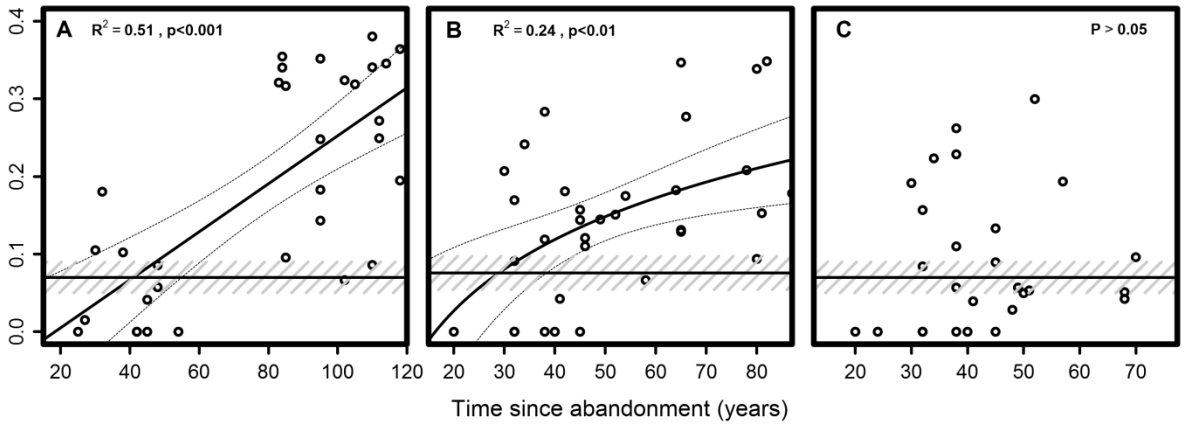


Figure 20. Functional dispersion (FDis) results for the tree tier in kānuka (A), fuchsia (B) and māhoe (C) forests over increasing recovery time. Standard regression methods were used to calculate model lines (mean + CI 95%) if significant trends over time were displayed ($p < 0.05$). The horizontal line indicates mean values for the reference site (red beech forest) and the shaded area depicts the standard error of the mean.

Table 18. Mean ± SE for all tested functional attributes are shown for each vegetation trajectory and the reference forest. If linear models results were significant ($p < 0.05$), mean ± SE for the oldest recovery age per forest type are given, or if not, the mean (± SE) across all plots is depicted. Statistical significance is indicated by: ns (non-significant) =p > 0.05, *=p ≤ 0.05, **=p ≤ 0.01, *** = p ≤ 0.001. Appropriate data transformations were applied (see Appendix 11 for model details). *See Table 16 for an explanation of index abbreviations used.*

		Kānuka	Māhoe	Fuchsia	Reference
Growth form	Medium trees	0.32 ±0.17***	0.99 ±0.01***	0.96 ±0.24***	0.06 ±0.02
	Shrubs	0.27 ±0.11***	0.02 ±0.04***	0.02 ±0.24***	0.05 ±0.03
	Small trees	0.06 ±0.16ns	0.01 ±0.01ns	0.08 ±0.01ns	0.00 ±0.00
	Large trees later	0.02 ±0.00ns	0.00 ±0.00ns	0.11 ±0.01ns	0.89 ±0.04
	Large trees early	0.40 ±0.26***	0.03 ±0.01ns	0.05 ±0.08*	0.04 ±0.03
Dispersal	Bird	0.53 ±0.17***	0.76 ±0.21***	0.98 ±0.24***	0.16±0.05
	Wind	0.42 ±0.17***	0.04 ±0.01na	0.11 ±0.01ns	0.84±0.05
	Gravity	0.01 ±0.00ns	0.01 ±0.22***	0.03 ±0.20***	0.00±0.00
Indices	FRic (tr)	0.16 ±0.05*	0.04 ±0.01ns	0.13 ±0.05**	0.10 ±0.0378
	FDiv (tr)	0.92 ±0.02ns	0.66 ±0.05ns	0.76 ±0.04ns	0.82 ±0.0534
	RaoQ (tr)	0.11 ±0.03***	0.02 ±0.01ns	0.06 ±0.03*	0.02 ±0.0057
	FDis (tr)	0.29 ±0.04***	0.09 ±0.02ns	0.21 ±0.08**	0.07 ±0.0202
	FEv (tr)	0.8 ±0.17***	0.63 ±0.07ns	0.62 ±0.04ns	0.45 ±0.0867
	FGR (tr)	4.32 ±1.01***	2.89 ±0.08*	3.85 ±0.85***	1.82 ±0.2429
	FGR (sh)	6.97 ±1.20***	4.78 ±0.9***	4.54 ±1.49**	4.86 ±0.3499
	FRic (sh)	0.13 ±0.04***	0.04 ±0.01ns	0.05 ±0.01ns	0.11 ±0.0108
	FDiv (sh)	0.78 ±0.02ns	0.56 ±0.15*	0.76 ±0.03ns	0.84 ±0.0254
	RaoQ (sh)	0.05 ±0.01***	0.04 ±0.01ns	0.04 ±0.01ns	0.04 ±0.0027
	FDis (sh)	0.22 ±0.04***	0.21 ±0.08**	0.19 ±0.08**	0.17 ±0.0105
	FEv (sh)	0.69 ±0.10*	0.65 ±0.04ns	0.68 ±0.04ns	0.60 ±0.0393

5.5. *Discussion*

Species Diversity

In this study species diversity indices, especially species richness showed the strongest trends over recovery time of all three diversity index groups tested. They are also highly correlated with each other, as has been noticed in other studies (Magurran 2004; Morris et al. 2014). Hence, index choice seems to be less critical for simple analyses as observed by others (e.g. Morris et al. 2014). Species diversity indices were also correlated with measures such as average taxonomic diversity (Δ) and functional dispersion (FDis) from other groups. As expected, reference forest values were reached after a short time and were higher at the end of the observation time for all secondary forests. Anthropogenic disturbances are known for their potential to increase species diversity, due to the higher

presence of generalist species which retain better adapted dispersal strategies than later seral plants (Buckland et al. 2005; Mayor et al. 2015).

The two evenness measures applied suggested that both broadleaved trajectories become more uneven with time, whilst the reference site displayed high species evenness. However, these results have to be regarded with caution, as high species evenness seemed to be correlated with very low species numbers. The construction of biodiversity profiles or the examination of indices following Hill's series have been frequently suggested to allow a more in-depth understanding of ecosystems processes (Heip et al. 1998; Leinster & Cobbold 2012; Morris et al. 2014), but in this study they did not add further information to Simpson's evenness.

One common issue for the diversity and evenness indices was which value to assign to plots with only one species present. Simpson's evenness gave the highest value in this case (e.g. 1), showing that the community was very even. All species diversity indices transformed into relative species numbers generated an index result of one. When their diversity profile is inspected, the flat curve would be interpreted as being highly even. Obviously, the results in both cases are wrong. This issue is known to be caused by indices being highly dependent on species richness (Heip et al. 1998). However, the early successional plots tend to hold often just one pioneer species (e.g. kānuka, gorse), but cannot be disregarded from the analysis if evaluating diversity change over a successional trajectory. Species diversity and evenness measures seem to receive the most attention in species rich environments and it might be that they are of less use in species poor ecosystems (the author is not aware of a publication regarding this question). In this case, these indices might be unsuitable for restoration plantings that hold a limited number of species over a foreseeable period of time. Information gained by inspecting these species diversity and evenness indices is, however, rather limited. Forest succession is still in a very early stage along all three trajectories, but indices results ranked these forest types higher than the reference site. This is a result of generalist species with dispersal strategies adapted to disturbances being more widespread and/or a higher availability of resources, such as light, which would have been previously limited (Buckland et al. 2005; Swanson et al. 2011). The fast recovery of woody plant diversity to reference values has been noted in other restoration projects (e.g. Aide et al. 2000; Fang & Peng 1997; Parrotta & Knowles 1999). This effect is usually present in early forest successional stages, followed by a drop in diversity caused

by resources becoming more limited over time (Schoonmaker & McKee 1988). This could render the application of these indices over short time frames, currently common in restoration projects, as inadequate. They also did not differentiate well between a forest undergoing a transition into the next successional stage (kānuka), and one that is in a stable stage (fuchsia/māhoe).

Taxonomic Diversity

Warwick and Clarke suggested that taxonomic diversity indices are less sensitive to sample size than traditional species diversity indices and might retain more sensitivity towards anthropogenic disturbances (K. R. Clarke & Warwick 2001; Warwick 2008; Warwick & Clarke 1995).

This study can confirm other studies which found average taxonomic diversity (Δ) to be correlated with species diversity measures (Heino et al. 2007; Merigot et al. 2007). This is not surprising as Δ is empirically related to Simpson's species diversity index (Warwick 2008). As the response shape over time is very similar to the species measures, it seems to add little new information to it. The observed weak correlation of taxonomic distinctness (Δ^*) with species diversity measures is also in agreement with other studies (von Euler & Svensson 2001). Nevertheless, contrary to species indices, taxonomic distinctness has been shown to be effective in detecting signals of stress in different ecosystems in some studies (von Euler & Svensson 2001; Warwick & Clarke 1998), whilst others reported no relationship or unpredictable behaviour (Bhat & Magurran 2006; Roque et al. 2014). It is interesting that the index registered some of the still grazed plots that are located outside Hinewai Reserve, displaying higher values. The effect might be caused by the higher abundance of *Podocarpus laetus* outside of Hinewai, producing a high Δ^* value as it belongs to the class *Pinopsida* whereas all other trees belong to the class *Magnoliopsida*. However, due to limited data on the grazed sites (control) outside of Hinewai, no further statistical analysis was undertaken. The funnel plots recommended by Warwick and Clarke (1998) did single out some sampling plots as being more degraded than others, but the reason for this was not apparent. Variation in taxonomic distinctness (Λ^+) was also confounded with species indices and its interpretation was found to be difficult. Index values increased over time and were found to be higher (tree tier) or lower (shrub tier) in the secondary forests than in the reference forest. Communities are becoming thus more or less taxonomically distinct. It is nevertheless not entirely evident if this is rather positive or negative in forest settings, or what one would generally expect.

The application of taxonomic diversity indices has been limited, and they have mostly been used in marine or freshwater ecosystems focusing on invertebrates. In addition, it is not fully understood at which observation scale they are most effective (Roque et al. 2014). In forest restoration settings, this has been their first application (to the knowledge of the author) and more research is required to clarify their suitability.

Functional Measures

One issue with functional diversity indices is that they are highly dependent on the traits selected as input values. It is then difficult to assess if the low trends observed over time within the forest types are genuine and can be attributed to the relatively short observation time frame or if, alternatively, they are due to choosing inappropriate traits. The traits were selected with respect to plant resilience to potential stressors and as dominance measures, meaning the higher the diversity the higher the probability that the system persists in cases of disturbance. The reference forest received the lowest values in almost all indices for the tree tier, but it also had the highest variance in the data. Kānuka showed the strongest trend with increasing recovery time, whereas the broadleaved trajectories displayed only very limited change. As the strong temporal trend in tree richness was only weakly reflected in the functional indices for the broadleaved forests, functionally similar species must have been entering the succession. As already noted, the broadleaved species (e.g. māhoe, fuchsia) which gain increasing dominance within the research area, possess dispersal as well as establishment advantages over later successional species (e.g. *Fuscospora fusca*) at a certain disturbance level. The traits selected here are therefore biased towards these species, which obviously retain a higher resilience towards some level of disturbance. Hence, the lower index results for the reference site. However, the functional indices were found to be strongly correlated with species diversity indices. The reason that māhoe and beech had low index values could simply be a fact of lower tree richness in both forests. Likewise, the fact that the reference site reached similar or even higher index values for the shrub tier, might be caused by either a similar species richness for beech and the broadleaved forests, or by recruiting similar (broadleaved) species.

Development of individual functional groups over time showed, at least for growth form and dispersal mode, a clearer trend that is easy to interpret. It also revealed the scarcity of later successional species (*Fuscospora* sp. and Podocarpaceae) in all vegetation tiers in the study area. This, together with the

known dispersal limitations of beech, indicates that the system is somehow arrested and it is not clear over what time frame it will develop into beech – podocarp forest. Since the percentage of bird-dispersed woody plants increased over time, within all fruit sizes, it is unlikely that dispersal is the limiting factor for *Podocarpus* or *Prumnopitys* species.

5.6. *Summary*

The number of biodiversity indices is still increasing rapidly in the literature, in particular for functional indices. This research tested commonly used indices belonging to three broad groups of biodiversity measures: (i) species, (ii) taxonomic and (iii) functional. In addition, (iv) single measures of functional group membership were investigated. This study showed that species diversity indices are easy to calculate and relatively straight forward to interpret with little differences in results between them. The other two groups of indices are more challenging. Unfortunately, in the context of Hinewai Reserve, the information gained by the species diversity indices did not show a realistic picture of convergence towards the reference system. This might be a result of the natural low species richness present in this ecosystem. Hence, results of this study indicate that the application of these indices in naturally low-richness forests might be inadequate.

The taxonomic distinctness (Δ^*) measure, which displayed more interesting trends, suffers from being mostly untested in forest ecosystems and was especially difficult to interpret. The functional indices showed only very weak to moderate trends over the recovery time. The reason is not entirely clear, but might be connected to either an observation time that is too short or the recruitment of functionally similar species over time within the broadleaved trajectory. The functional indices in particular suffer from several pitfalls for the inexperienced user (i.e. which traits and how many to choose) and have also largely been tested in theoretical situations only. The clearest and easiest results to interpret, with the highest information content, provided the individual inspection of species (functional) groups such as late successional trees over recovery time. They may therefore be, with other carefully chosen structural plant and compositional measures, currently the best choice for restoration projects, especially if applied for biodiversity offset situations that require easy to interpret and transparent measures.

Chapter 6
Linking Aboveground and Belowground Measures for the Assessment of Restoration Success

6.1. *Abstract*

The importance of belowground measures for the assessment of restoration success has been frequently noted. For biodiversity offsets in particular, the question arises; how well does the recovery of vegetation relate to belowground biota and the ecological functions they perform? Most of the biodiversity is located in the litter and soil layers of forests, not within the vegetation. Soil biotas are a major driver of litter decomposition, an import process within the nutrient cycle. This chapter examines how the state of vegetation recovery relates to leaf litter invertebrate diversity and community composition. The relationship between the functional group of decomposers and leaf litter decomposition was assessed, to establish if there is indeed a measurable link. Patterns in litter invertebrate diversity and composition were weak and did not follow the vegetation trajectories in a predictable manner, as they differed between the two successional pathways. There was also no relationship between decomposer abundance or diversity and leaf litter decomposition. Soil attributes advanced in a predictable manner and provided better, easier to measure estimates of the nutrient cycle. Anaerobic mineralisable nitrogen content related especially well to leaf litter decomposition, as did the pH value. The ecology of soil and litter biota is still not well understood but very sensitive to small-scale differences in the environment. Until much progress has been made to better understand these processes, belowground biotas are likely to remain, for the largest part, a black box for restoration projects.

6.2. *Introduction*

Ecological restoration has historically focused on aboveground measures, primarily vegetation structure and composition (Young 2000). These attributes are often assumed to act as a proxy for the overall ecosystem condition and biodiversity of other groups (Hilderbrand et al. 2005). Research has shown that in some cases where vegetation has been restored, soil ecology is not necessarily restored at the same time, (Ballantine & Schneider 2009; J. A. Harris 2003; P. Kardol et al. 2005). Despite the aim of biodiversity offsets being to quantify and

restore site biodiversity, this disparity is frequently overlooked, even though it is the soil that holds most of the biodiversity in any given site (D. A. Wardle 2002).

Over recent years, however, the importance of the inherent link between belowground and aboveground processes for restoration ecology has been emphasized (Callaham et al. 2008; Eviner & Hawkes 2008; Paul Kardol & Wardle 2010). Fundamental ecosystem functions such as organic matter decomposition and recycling of nutrients occur in the soil and have a profound effect on the vegetation above. Dynamics in the leaf litter and soil organic matter layer play a key role in these processes and represent at the same time diversity and functional hot spots in forest ecosystems (Hansen 2000). Besides climatic conditions, soil organism activity is an important driver of decomposition of plant organic matter (Lavelle 1997; Wallwork 1970). In turn the vegetation, determining the quality and quantity of resource input can have a large effect on abundances and diversity of soil / litter biota and, as a result, on decomposition and soil formation (D. A. Wardle 2002). However, the direction and strength of this relationship seems to be context dependent and might affect soil faunal groups differently (D. A. Wardle et al. 2004, 2006).

Progressing plant succession is often tightly coupled with changes in soil chemical and physical aspects. The link between vegetation and soil or litter community recovery is less well understood (D. A. Wardle 2002). Their importance for litter decomposition is often emphasized (e.g. Cole et al. 2016; Snyder & Hendrix 2008), but it is not entirely clear if there is a direct measurable link between them. Can the condition of leaf litter invertebrates be derived from simple vegetation and ecosystem process measures; or is there no alternative but to assess this fauna directly? Also, is it even possible to assess the recovery of these invertebrates in a meaningful way in restoration projects?

This study focuses on meso- (100µm - 2mm) and macro-invertebrates (size > 2mm) present in the leaf litter. These invertebrates perform the first part in the litter decomposition process, shredding and fragmenting litter and maintaining soil structure. They also regulate fungal and microfaunal populations (Coleman et al. 2004). Despite inhabiting a wide range of functional roles and holding a high diversity of different taxa (sensu Briones 2014 for a review), meso- and macro-invertebrates have received little attention (apart from earthworms) and their response to restoration strategies or succession is generally not well known (Cole et al. 2016; Snyder & Hendrix 2008). Depending on the level of taxonomic identification required, they are also notoriously difficult to identify and

generally very labour intensive to work with. Many taxa are still not described and even for described taxa often little is known about their ecological requirements. To overcome some of these difficulties, invertebrates were sorted into recognisable taxonomic units. This approach is generally faster than identifying to actual species, requires no specialists and has been shown to accurately describe the number of real taxa for several key groups (e.g. Derraik et al. 2002; Oliver & Beattie 1996).

This chapter examines trends in the following ecosystem attributes: (A) leaf litter macro-and meso-invertebrate diversity and composition, (B) soil processes such as formation of soil organic matter and (C) leaf litter decomposition over two main vegetation successional trajectories. Their similarity to a reference forest (red beech old growth) after 120 (kānuka trajectory) and 87 years (mixed-broadleaved trajectory) are reviewed. The following questions were specifically investigated:

(i) Are attribute trends following the same pattern across the two vegetation trajectories (i.e. are they predictable) or are there significant differences between the two trajectories?

(ii) Does the diversity or composition of the invertebrate community or particular taxonomic or functional groups within the invertebrate community reflect the trend of progressing vegetation succession moving along the two forest trajectories? (i.e. can vegetation measures such as diversity or composition be used as a proxy for leaf litter invertebrate recovery)

(iii) Is there a correlation between litter invertebrate diversity and compositional recovery and more easily measured ecosystem attributes such as leaf litter decomposition or soil variables (i.e. can these attributes act as a proxy for leaf litter invertebrate recovery)? Specifically, is decomposer diversity linked to decomposition rates as it has been hypothesized by D. A. Wardle (2006)?

(iv) Do attributes investigated converge over time to reflect those of the reference site; hence, has restoration success been achieved?

6.3. *Methods*

6.3.1. Leaf Litter Invertebrates

Leaf litter invertebrates were sampled from December 2012 to January 2013, subsequent to a pilot study in November 2012 used to develop the sampling method and determine required sample size. A 30cm x 30cm metal quadrat was placed 2 m northwards of each plot centre (n = 105). All leaf litter within this quadrat was scraped off until the mineral soil was reached. The litter obtained was subsequently vigorously sieved for 3 minutes to extract the invertebrates, separating the litter into a fine and coarse fraction. Total coarse and fine volume of leaf litter was measured with a measuring jug. The sieved fine litter material was placed in paper bags and transported back to the lab in chilly bins.

These samples were immediately placed in 50 Tullgren funnels, which were designed and built by Dr Steve Pawson from Scion Christchurch (New Zealand Forest Research Institute Limited) from milk cartoons, lampshades, light bulbs a funnel and mesh screen (Figure 21). This extraction method works by placing leaf litter on a fine mesh with a heat/light source (light bulb) above, which invertebrates then moved away from, down into a funnel to be collected in a small jar with 75 % ethanol below. Funnels were operated for 48 hours and samples were subsequently hand-checked for any invertebrates that did not move through the funnels (especially Amphipoda). Leaf litter samples were then oven dried at 70 °C for at least 48 hours until the weight stabilised to obtain dry mass weight. Dry mass weight was used to estimate the total water content of the samples.

Invertebrates were sorted to order level using the key to New Zealand soil and litter invertebrates (Minor & Robertson 2006) and were identified down to unique recognisable taxonomic units (RTUs). Basic invertebrate taxonomic training has been shown to improve results of sorting to RTUs (Barratt et al. 2003) and was provided by entomologist Dr Tara Murray. Three taxonomic groups were identified further down to family or genus level. This was done for (i) Coleoptera (beetles), to enable the assignment to feeding groups. For (ii) Diplopoda (millipedes) being important representatives of the functional group of shredders (a subgroup of decomposers), which stimulate microbial activity through fragmentation of organic debris. Millipedes have also been suggested as proxies for overall decomposer diversity (Gerlach et al. 2013), as indicators of soil restoration success (Snyder & Hendrix 2008) and ecosystem stress because they

are sensitive to changes in land use and litter moisture gradients (sensu Paoletti et al. 2007). The last group identified down to family level were the (iii) Chilopoda (centipedes). Centipedes usually represent the most abundant predators in leaf litter in temperate forests (Ferlian & Scheu 2014) and might have a significant influence on litter decomposer communities (Kalinkat et al. 2013; Salmon et al. 2005), thus might profoundly influence ecosystem function.

The identification and assignment to functional groups were based for beetles on the family key to New Zealand Coleoptera (Klimaszewski & Watt 1997), for centipedes and millipedes on unpublished and published keys of Johns (1962, 2015a, 2015b) to New Zealand taxa, and for spiders (Araneae) on the key published by Paquin et al. (2010). Entomologist Peter Johns identified all millipedes and centipedes; he further checked the author's identification of all other groups with the exception of spiders and worms (Annelida). Ten weevils RTUs were checked by Barbara Barratt (AgResearch) to confirm if they were distinct enough to represent different RTUs. However, the author of this thesis alone is responsible for any identification error that might have occurred. The extensive checklist on insects and other arthropods present at Hinewai Reserve (J. B. Ward et al. 1999) was also used for cross-checking identifications and to gain information about species biology.

Figure 21. Tullgren funnel set up, using a lampshade, milk cartons, and light bulbs to extract invertebrates into the 75 % ethanol solution placed below.

Functional groups for invertebrates other than beetles, millipedes, centipedes or spiders were assigned based on the functional role which most of the taxa members generally perform (Coleman et al. 2004).

6.3.2. Ecosystem Function

Soil

Soil samples were taken from 50 sampling plots on an overcast day in November 2013 (Table 19). The sample size was initially set to be 10 per successional stage, but could not be achieved because one sample was lost in the lab and eight samples were reassigned to different successional stages between sample collection and analysis: for information on reclassification of successional stages see Chapter 3. From four randomly chosen locations within a sampling plot, leaf litter/humus was removed and the upper 10 cm of mineral soil were collected. The four samples were mixed to achieve a composite sample and sieved with a 4 mm sieve. Soil temperature was also measured at each sampling plot. In the field, as well as on their way to the lab, samples were transported in a chilly bin on ice. Soil samples were analysed for their: pH, total organic carbon (C), total nitrogen (N), C:N ratio, anaerobic mineralisable nitrogen (min N) and Olsen phosphorus (P). Olsen P as a measure of plant-available phosphorus was chosen as both successional pathways investigated here originate from pasture. This measure is greatly affected by fertiliser additions, and hence might indicate prolonged effects of site management. Anaerobic mineralisable nitrogen represents a measure/index of microbial activity and was selected over an alternative measure, basal respiration, as it usually has a smaller within-plot variation (pers. comm. Craig Ross 17.9.2013, Landcare Research). All chemical analyses were done in the Landcare Research environmental chemistry laboratory in Palmerston North. For detailed information about lab procedure for each measured soil variable see the Landcare website (http://www.landcareresearch.co.nz/resources/laboratories/environmental-chemistry-laboratory/ services/soil-testing/methods#132).

Table 19. The total number of sampling plots and number from which soil samples were collected per successional stage at Hinewai Reserve. Māhoe (*Melicytus ramiflorus*) and fuchsia (*Fuchsia excorticata*) represent alternative states along the mixed-broadleaved trajectory. Old growth refers to the red beech forest (*Fuscospora fusca*) used as a reference site. Due to limited sample sizes, the three oldest stages of the mixed-broadleaved forest were merged into one group for the analysis.

	Successional stage	*n* plots	
		Soil	Total
Broadleaved	Pasture	0	5
	Gorse	10	11
	Emergent natives	0	10
	Māhoe	3	12
	Fuchsia	5	16
Kānuka	Early kānuka	10	13
	Intermediate kānuka	5	9
	Late kānuka	6	11
	Reference forest	10	17

Leaf Litter Decomposition

The leaf litter bag technique was applied to estimate relative differences in litter decomposition between successional stages (Bocock & Gilbert 1957). Fresh red beech (*Fuscospora fusca*) leaves were harvested in Hinewai Reserve. Leaves were cleaned and air-dried at around 20 °C for two weeks in March 2012. Non-decomposable plastic material was cut into approx. 3 x3 cm segments and used as control filling. This filling was employed to correct for bag contamination by foreign material like soil and roots. Nylon bags (15 x 20 cm) were filled with 3 g of either dried leaves or the control material. Bags featured a finer bottom mesh size (1 x 1 mm), to prohibit leaf loss and a coarser mesh on top (3 x 3 mm), to ensure that macrofauna could enter (Paul Kardol et al. 2006). At each of the 108 sampling plots located at Hinewai Reserve, three replicate leaf litter bags plus one control bag were installed in April 2012 (Figure 22). After removing the litter layer, bags were placed on the ground 1 m away from the plot centre, facing north, east, west, and south (Figure 22). To ensure good soil contact and secure them from animal removal, bags were anchored with two metal pins. Four test bags were permanently retrieved after 1 year, but as weight loss was low the decision was made to leave them a further 6 months in the field. Bags were finally retrieved in October 2013. Their content was thoroughly cleaned and oven dried at 50 °C for 5 days to a constant weight. Dry weight was corrected with the mass gain observed for the control bags for each plot individually. Finally, not decomposition rate but mean weight loss (g) per plot was calculated. This approach was chosen as the focus of this study was on the relative decomposition differences between vegetation types rather than on absolute decomposition.

Figure 22. Example of four leaf litter bags placed at each sampling plot; three were filled with 3 g dried red beech leaf litter and one with 3 g of non-decomposable material as a control to correct for foreign material growing into the bags.

6.4. *Analysis*

6.4.1. Leaf Litter Invertebrates

A high variability in the number of individual invertebrates observed per plot, between successional stages (Table 20) and low overall numbers for most taxonomic groups were encountered. To account for this issue, successional stages (two main trajectories) rather than recovery time was used in all analyses to increase statistical power.

Table 20. The overall number of plots sampled (n) and invertebrates extracted per successional stage.

	Successional Stage	n	Invertebrate counts	
			Total	Mean±SD
Broadleaved	Pasture	5	1027	207±108
	Gorse	11	1410	126±66
	Em. Natives	10	7938	723±1257
	Māhoe	13	4312	360±600
	Fuchsia	20	10882	519±1135
Kānuka	Early Kānuka	12	5542	265±403
	Intermediate Kānuka	19	5022	402±795
	Late Kānuka	13	4419	291±314
	Reference forest	22	7007	207±108

Richness and Diversity

Species richness, i.e. the total number of species (N_0), and two indices considering the number of species present and their relative abundances, Shannon's (N_1) and Simpson's diversity (N_2) (see Chapter 5: Table 15 for definitions), were investigated. 'Effective' rather than actual number of species were used to calculate three diversity indices, providing easier to interpret results (Jost 2006; Morris et al. 2014). Effective species refer to the number of equally abundant species required in a community to provide the observed diversity index results (Jost 2006). Indices calculated this way are also known as Hill's numbers (Hill 1973). N_0-N_2 assign decreasing weight to rare species and can be used in combination to inspect the degree of dominance present in the community (Morris et al. 2014).

All three diversity attributes were calculated for the decomposers (i.e. all RTUs assigned as decomposers across all taxa) as well as for the beetle and spider taxa separately, being the only groups having more than 20 RTUs in total. Beetle functional groups were also analysed separately. RTUs are referred to as species throughout this chapter.

As total invertebrate catches per sample were low, data were pooled for each successional stage before analysis to increase statistical power, as recommended by Chao et al. (2016). As a consequence, differences in vegetation group means across forest trajectories were analysed, rather than change over recovery time. Because of the well-known species area relationship (sensu McGuinness 1984), observed species richness can only be accurately compared between communities if species accumulation curves show a clear asymptote (Gotelli & Colwell 2001; Sanders 1968). For many vegetation and all taxonomic groups, sample completeness curves indicated insufficient sampling effort as no such asymptote had been reached (Appendix 14).

Hence, species data had to be standardized to a common sampling effort. Sampling effort is traditionally standardised to either area sampled or individuals counted. Rarefaction standardises to the lowest observed sample size, while extrapolation estimates species diversity up to its asymptote. For this research, a recently developed method to rarefy species richness and Shannon and Simpson indices to a common percentage of sample completeness was applied to achieve standardisation (Chao et al. 2014; Chao & Jost 2012).

Sample completeness or coverage refers to the proportion of the total population represented by the observed species in a sample (Jost 2010). It provides an unbiased representation of differences in diversity magnitudes between communities (Chao & Jost 2012). Whilst traditional standardisation methods (e.g. by sample size) give an incomplete characterisation of communities caused by the unequal representation of the total species pool at a certain sample size (Chao & Jost 2012). Estimating differences in species diversity based on sample completeness is regarded as a robust and reliable method if at least a sample coverage of 50 % is obtained (Chao & Jost 2012; Chao & Lee 1992). Sample completeness curves showing sample coverage over increasing sampling effort (number of individuals) were inspected instead of classical species area curves to estimate sampling effort. All diversity calculations were done on individual-based abundance data. The mean and its 95 % confidence interval were calculated for Hill's numbers: species richness, Shannon's and Simpson's indices by using bootstrapping with 100 replications. For beetles, beetle functional groups and spiders, sample coverage was separately rarefied to the lowest observed value for all successional stages. The R package 'iNEXT' was used for calculating all richness and diversity indices and to create related plots (Hsieh et al. 2016).

Composition

Beetles represented the most diverse taxon in this study, and hence trends in overall beetle composition and by functional groups (herbivores, decomposers, predators) were investigated. In addition, compositional change in decomposers across all taxa was analysed to see how well these trends linked to leaf litter decomposition and major soil processes. There were too few spider species per sample to conduct a meaningful analysis. To reduce the noise and to intensify the signal of the overall trend for all other groups, species which appeared in less than 10 percent of the samples were excluded from the analysis (McCune & Grace 2002). All analyses were carried out on untransformed abundances using the Bray-Curtis dissimilarity (J Roger Bray & Curtis 1957) as well as presence/absence only data using the Jaccard similarity (Jaccard 1912). The Bray-Curtis coefficient has been shown to outperform most other resemblance measures especially in practical applications, hence its widespread use among ecologists (K Robert Clarke et al. 2006). Presence/absence data were investigated to overcome (unrecorded) small-scale site conditions resulting in differences in species abundances. At first, compositional differences between successional stages along the two main trajectories were examined using a Permutational

Multivariate Analysis of Variance (PERMANOVA) (Anderson 2001). As a prerequisite, multivariate homogeneity of group variances was confirmed using a multivariate analogue of Levene's test (package 'vegan' (Oksanen et al. 2016), function 'betadisper'). Equality of variances among groups is the important underlying assumption of PERMANOVA, which is otherwise susceptible to confusing differences in group locations with their dispersion (Anderson & Walsh 2013). This non-parametric method uses distance/dissimilarity matrices to partition variation among individual model terms and is therefore analogous to multivariate analysis of variance (MANOVA). Type II PERMANOVA, testing each main effect after the other, was used as recommended for unequal sample sizes (package RVAideMemoire (Hervé 2016), function 'Adonis.II'). The PERMANOVA procedure was first applied separately on each of the two vegetation trajectories to test for the overall effect of successional stage on species composition. If vegetation types had a significant effect on species assemblages, groups in each trajectory were then tested pairwise (package 'RVAideMemoire' (Hervé 2016), function 'pairwise.perm.manova') and *p*-values were corrected for multiple comparisons using the method developed by Benjamini and Hochberg (BH) (1995). To investigate the underlying drivers of compositional change in more detail, stepwise model selection on a PERMANOVA was undertaken. All potential confounding and covariate variables (Table 21) as well as vegetation types were tested.

To visualize results, non-metric multidimensional scaling (NMDS) ordinations were used (package vegan, function 'metaMDS'). NMDS ordination is generally regarded to be the most robust unconstrained ordination technique for ecological data (Faith et al. 1987; McCune & Grace 2002).

Table 21. List of covariates (habitat) and confounding (environmental, sampling date and spatial coordinates) variables used in conjunction with either successional stage or recovery time (leaf litter decomposition) in linear models, ordinations and PERMANOVAs.

Variables	Units
All plots	
Sampling date	
Spatial Coordinates (NZTM)	
Slope	°
Aspect	transformed into eight classes (e.g. N, NE, E)
Physiography	gully, terrace, face, ridge
Altitude	m
Total leaf litter volume	$cm^3/900cm^2$ (measured in the field)
Leaf litter moisture	% (proportion fresh/dry weight of leaf litter in bags)
Detritivore abundances	count per sample
Canopy cover	% (Chapter 5)
Shrub cover	% (Chapter 5)
Tree richness	(Chapter 4)
Basal area of māhoe & fuchsia	$m^2\ ha^{-1}$ (Chapter 5)
Basal area of kānuka	$m^2\ ha^{-1}$ (Chapter 5)
Coarse woody debris	$m^3\ ha^{-1}$ (Chapter 5)
Only for soil data subset	
Soil temperature	°C
pH	
Olsen P	$mg\ kg^{-1}$
Total organic carbon	%
Total nitrogen	%

6.4.2. Ecosystem Function

Soil

Soil data was only available for 49 sampling plots. Welch's ANOVA was used to test for differences in measured soil attributes between successional stages (Welch 1947). Due to the limited sample numbers for each successional stage along the mixed-broadleaved trajectory, māhoe, fuchsia, and emergent natives were analysed as one group (mixed-broadleaved forest). This was done separately for each of the two trajectories. Welch's correction was chosen as it tolerates non-homogeneous variances across groups which might occur due to the unbalanced design /small sample sizes in this study (Moder & Moder 2010). First, an overall ANOVA investigating differences across all successional stages was carried out. Normality of attributes was inspected using quantile - quantile plots. If necessary, log transformation was used to attain normality. In the case that the overall ANOVA was significant, differences between individual groups

were subsequently tested by using the post-hoc Games Howell test with *p*-value corrections (BH) for multiple comparisons. Relationship between soil variables was investigated using Spearman's rank order correlation.

Leaf Litter Decomposition

For comparability with earlier chapters, the overall effect of time since abandonment on total weight loss was tested. A standard multiple regression approach, including all potential covariates (Table 21) was used to model leaf litter mass loss over time. Stepwise model selection was undertaken and non-significant terms were dropped from the model if model R^2 change was < 5. Overall quality of the reduced models was compared using the Akaike information criterion (AIC) (Akaike 1973). Multicollinearity of variables was assessed by calculating the variance inflation factor (VIF) and by inspecting coefficient error values. This is important as multicollinearity inflates error rates of coefficients, causing false statistically non-significant results.

For comparability with the other attributes assessed in this chapter, leaf litter decomposition was also assessed at the successional stage level. The same procedure as described for the soil variables was applied. Lastly, the relationship between litter decomposition and (log10+1 transformed) decomposer abundances and composition was investigated, again by using standard multiple regression methods and PERMANOVA. All statistical analyses for this chapter were undertaken using R 3.3.1 (R Core Team 2016), specific packages used are indicated in the section above.

6.5. *Results*

6.5.1. Leaf Litter Invertebrates

A total of 47559 specimens were collected and sorted into 211 recognisable taxonomic units (Table 22). Amphipoda were the most abundant group representing 22.7 % of all individual specimens, followed by Diptera larvae (22.6 %) and adult beetles (17 %). The greatest diversity was observed for the beetles, with 72 RTUs representing 26 different families. Millipedes (a proxy for the decomposer community) were represented with six families; centipedes (representing the predator community) belonged to four families (Appendix 15).

Table 22. Summary of all invertebrate groups encountered, providing the lowest level of taxonomic identification realised, and the number of recognisable taxonomic units (RTUs) applied. Relative and absolute abundances for all samples are given, along with the frequency of occurrence across all samples (FO) and the associated functional groups. Herbivores include taxa feeding on living plants/ fungi.

Group (class, order)	Level of tax. ident.	RTUs	Abundance		FO (%)	Decomposers	Herbivore	Predator	Omnivore
			Total	Relative (%)					
Annelida (excl. Opisthopora)	Class	7	2072	5	58	7			
Annelida: Opisthopora	Order	3	230	1	27	3			
Arachnida: Araneae	Order	31	1631	3	80			31	
Arachnida: Opiliones	Family	10	320	1	30			10	
Arachnida: Pseudoscorpiones	Order	3	520	1	36			3	
Chilopoda: Geophilomorpha	Genus	2	1046	2	68			2	
Chilopoda: Lithobiomorpha	Genus	5	753	2	60			5	
Diplopoda: Chordeumatida	Genus	3	204	1	40	3			
Diplopoda: Polydesmida	Genus	5	1425	3	74	5			
Diplopoda: Polyxenida	Genus	1	96	1	5	1			
Diplopoda: Siphonophorida	Order	1	7	1	2	1			
Diplopoda: Spirostreptida	Order	1	16	1	5	1			
Entognatha: Diplura	Order	1	14	1	3		1		
Gastropoda: Pulmonata	Order	1	39	1	5		1		
Insecta: Coleoptera (adult)	Family	72	7973	17	95	9	41	22	
Insecta: Coleoptera (larvae)	Family	28	2140	4	84	6	11	10	
Insecta: Diptera larvae	Order	7	10912	23	94			7	
Insecta: Hemiptera	Order	4	785	2	53		4		
Insecta: Hymenoptera	Order	2	614	1	48			2	
Insecta: Lepidoptera larvae	Order	14	4060	8	71	14			
Insecta: Neuroptera	Order	1	1	1	1			1	
Insecta: Orthoptera	Order	1	1	1	1				1
Insecta: Thysanoptera	Order	1	353	1	29		1		
Insecta: Thysanura	Order	1	17	1	2		1		
Malacostraca: Amphipoda	Order	2	9948	23	88	2			
Malacostraca: Isopoda	Order	2	2223	5	66	2			
Symphyla	Order	1	158	1	21	1			
Turbellaria: Seriata	Order	1	1	1	1			1	
Total		211	47559						

Not only invertebrates themselves but also their habitat, the leaf litter, was highly variable within and between successional stages, indicating a wide range of microsite conditions present in each successional stage. A graphical summary of variables known to affect invertebrates is given in Figure 23. Welch's ANOVA did not report significant differences for soil temperature between successional stages (kānuka: $F_{(3,11.1)} = 0.4$, $p = 0.7$; mixed-broadleaved trajectory: $F_{(3,7.7)} = 1.4$, $p = 0.3$).

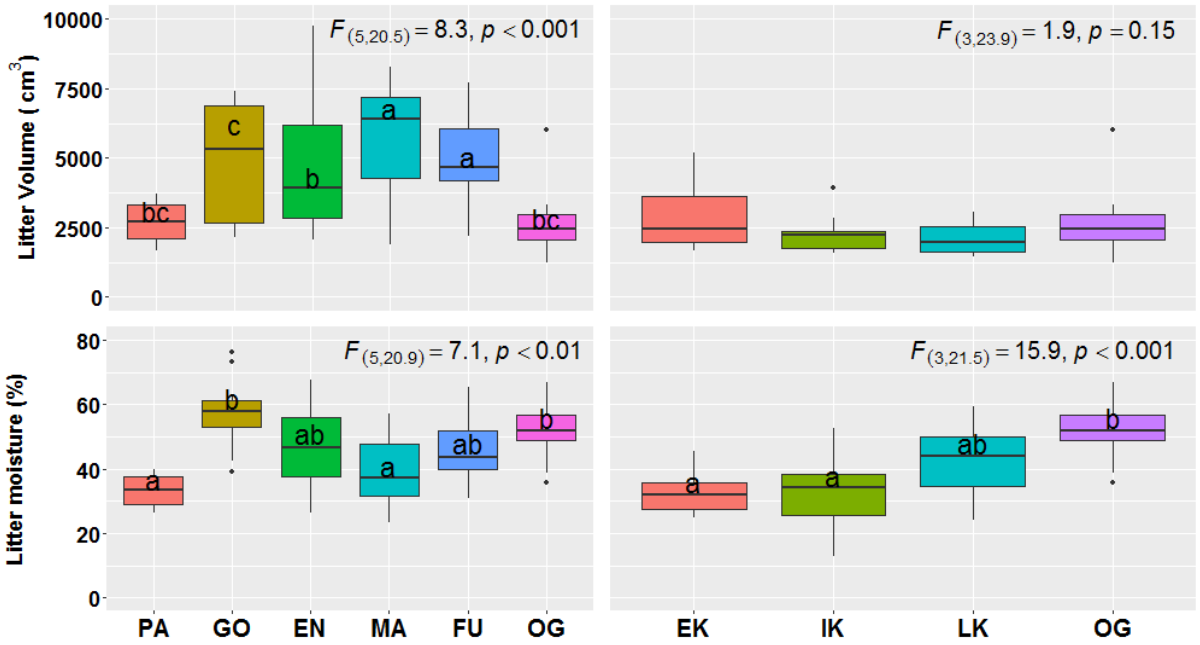


Figure 23. Variation in litter moisture and litter volume across successional vegetation stages for the two studied trajectories. Fresh litter volume (fine and coarse) is given per 900cm² (the quadrat) and litter moisture refers to the difference in dry/fresh weight of leaf litter material. The displayed F and P values indicate if significant differences were detected between any successional stages using an overall Welch's ANOVA. Boxes with the same letters indicate that individual successional stages were not significantly different from each other (post-hoc Games Howell test).

The following abbreviations were used for the two vegetation trajectories: (A) mixed-broadleaved forest: PA = pasture, GO = gorse, EN = emergent natives, MA= māhoe, FU =fuchsia; (B) kānuka forest: EK = early kānuka, IK = intermediate kānuka, LK = late kānuka; (C) reference site: OG = old growth.

Richness and Diversity

Beetles and spiders sample completeness was > 79% across all successional stages and as such observed data can be considered representative of actual diversity for these two taxa. However, sample completeness differed between successional stages (Appendix 14, Table 23). Therefore, for comparability across all successional stages results are presented only for estimated diversity data standardised to a common percentage of sample completeness.

Table 23. Observed and estimated diversity of pooled beetle and spider RTUs abundance data: N_0 = species richness, N_1 = Shannon index, N_2 = Simpson index. Estimated values were derived by coverage based rarefaction for all groups to the smallest sample coverage (SC) observed as described by Chao et al. (2014). The total number of individuals (n), and number of species which occurred only once (S) or twice (D) in a sampling plot are also shown. Non-overlapping confidence intervals (CI) for estimated diversity means can be interpreted as a significant difference in diversity at the 5 % level (see Appendix in Chao et al. 2016; Chao & Jost 2012), whereas overlapping CIs do not necessarily imply non-significant differences.

	Successional Stage	n	S	D	Observed		Estimated mean (95 % CI)			SC
					N^0	N^2	N_0	N_1	N_2	%
All Coleoptera	Pasture	39	16	7	24	9.6	15.0(10-19)	11.7(8-15)	9.6(6-13)	0.82
	Gorse	95	22	4	38	14.4	19.2(17-20)	15.3(14-17)	12.5(12-13)	0.93
	Em. Natives	186	21	10	43	6.2	15.0(13-17)	8.7(7-10)	5.7(5-7)	0.91
	Māhoe	137	25	6	38	6.6	18.9(16-22)	10.0(8-12)	6.1(5-8)	0.91
	Fuchsia	496	19	6	44	3.5	7.2(7-8)	4.5(4-5)	3.1(3-4)	0.98
	Early Kānuka	64	17	4	25	5.8	14.5(12-17)	8.9(7-11)	5.5(3-8)	0.89
	Int. Kānuka	113	18	11	35	15.6	18.7(17-20)	15.3(14-17)	12.9(11-15)	0.94
	Late Kānuka	160	18	6	32	3.4	10.3(8-12)	5.3(4-6)	3.2(3-4)	0.93
	Reference forest	175	16	9	46	15.8	23.2(21-25)	17.4(15-20)	13.5(11-16)	0.95
Herbivorous Coleoptera	Pasture	40	1	3	9	6.7	8.6(7-10)	6.4(5-8)	5(3-7)	0.97
	Gorse	84	5	2	17	13.9	16.9(14-20)	11.9(10-14)	9.5(7-11)	0.94
	Em. Natives	656	3	2	16	5.1	7.7(7-8)	4.5(4-5)	3.2(3-4)	0.94
	Māhoe	122	7	2	20	10.9	19.4(15-23)	10.8(9-13)	7.4(6-9)	0.94
	Fuchsia	579	5	0	21	7.8	13.5(13-14)	6.9(6-8)	4.4(4-5)	0.98
	Early Kānuka	272	2	0	15	9.3	11.1(10-12)	8.2(7-9)	6.7(6-8)	0.98
	Int. Kānuka	192	2	2	17	10.3	13.8(12-15)	9.4(8-10)	7.4(6-8)	0.98
	Late Kānuka	392	3	2	14	4.5	7.6(7-8)	3.9(4-4)	2.6(2-3)	0.98
	Reference forest	404	3	1	22	13.4	16.7(16-18)	11.8(11-13)	9.3(8-10)	0.98
Predatory Coleoptera	Pasture	7	0	2	3	2.9	2.7(2-3)	2.5(2-3)	2.3(2-3)	0.96
	Gorse	14	1	0	5	4.6	4.4(4-5)	4.1(3-5)	3.7(3-4)	0.99
	Em. Natives	16	2	2	6	4.9	5.6(4-7)	4.7(3-6)	4.1(3-5)	0.89
	Māhoe	18	2	0	3	1.5	2(1-3)	1.4(1-2)	1.3(1-2)	0.90
	Fuchsia	7	3	2	5	4.7	6.1(3-9)	5.9(3-9)	5.6(3-8)	0.64
	Early Kānuka	0			0		-	-	-	
	Int. Kānuka	19	1	0	3	2.2	2.0(2-2)	1.9(1-2)	1.7(1-2)	0.99
	Late Kānuka	12	2	0	5	4.4	4.5(3-6)	4.0(3-5)	3.7(3-5)	0.85
	Reference forest	18	0	0	2	15.8	1.7(2-2)	1.6(1-2)	1.5(1-2)	0.99
Araneae	Pasture	10	3	1	4	2.7	3.7(3-4)	3.4(3-4)	3.2(2-4)	0.91
	Gorse	24	6	3	10	2.2	9.3(7-12)	7.2(5-10)	5.6(4-8)	0.84
	Em. Natives	40	9	5	14	2.6	12.7(9-16)	8.7(6-12)	6.4(4-9)	0.82
	Māhoe	37	5	2	8	2.3	5.5(4-7)	3.0(2-4)	2.0(1-3)	0.95
	Fuchsia	15	2	0	3	1.7	2.4(2-3)	2.2(2-3)	2.0(2-3)	0.91
	Early Kānuka	48	10	1	13	2.2	9.5(7-14)	5.6(3-8)	3.9(3-5)	0.84
	Int. Kānuka	31	7	3	11	2.2	10.2(7-15)	7.3(5-11)	5.7(3-8)	0.81
	Late Kānuka	17	2	0	4	2.0	2.6(2-4)	2.3(1-3)	2.0(1-3)	0.94
	Reference forest	34	2	1	12	2.3	11.4(9-16)	6.3(3-10)	4.1(2-6)	0.80

Coleoptera

Overall

Most beetles encountered belonged either to the predatory Staphylinidae (36 %), the phytophagous Curculionidae (21 %) or Ptiliidae (16 %), and Zopheridae (9 %) which mostly feed on fungi (Klimaszewski & Watt 1997).

Estimated beetle diversity showed unpredictable patterns along the mixed-broadleaved trajectory (Figure 24). Fuchsia forest displayed the lowest values (N_0, N_1), whereas diversity in the māhoe forest was significantly higher. Māhoe displayed similar species richness as gorse but Shannon and Simpsons mean values were significantly lower, suggesting a high degree of unevenness across species. The mean values for all diversity indices were lower for all stages of the mixed broadleaved trajectory relative to the reference forest. This difference was significant compared to all successional stages except the māhoe forest. For the Shannon (N_1) and Simpson diversity (N_2) the data was inconclusive, as CI's were overlapping for several successional stages (reference forest: N_1 + N_2, gorse: N_1 + N_2, pasture: N_2).

The kānuka trajectory displayed a much clearer trend with diversity values peaking significantly in the middle aged (intermediate) stage and decreasing to the lowest values in the oldest stage (late kānuka) (significant for richness and Shannon). The distinct differences between the three diversity indices (N_0-N_2) indicate a high unevenness across species; a few species being numerically dominant whereas most were rare in the late kānuka beetle community (Figure 25. Unlike the mixed-broadleaved trajectory only species richness was significantly higher for the reference forest relative to the stages of the kānuka forest, whereas the Shannon and Simpsons indices, which give less weight to rare species, were not.

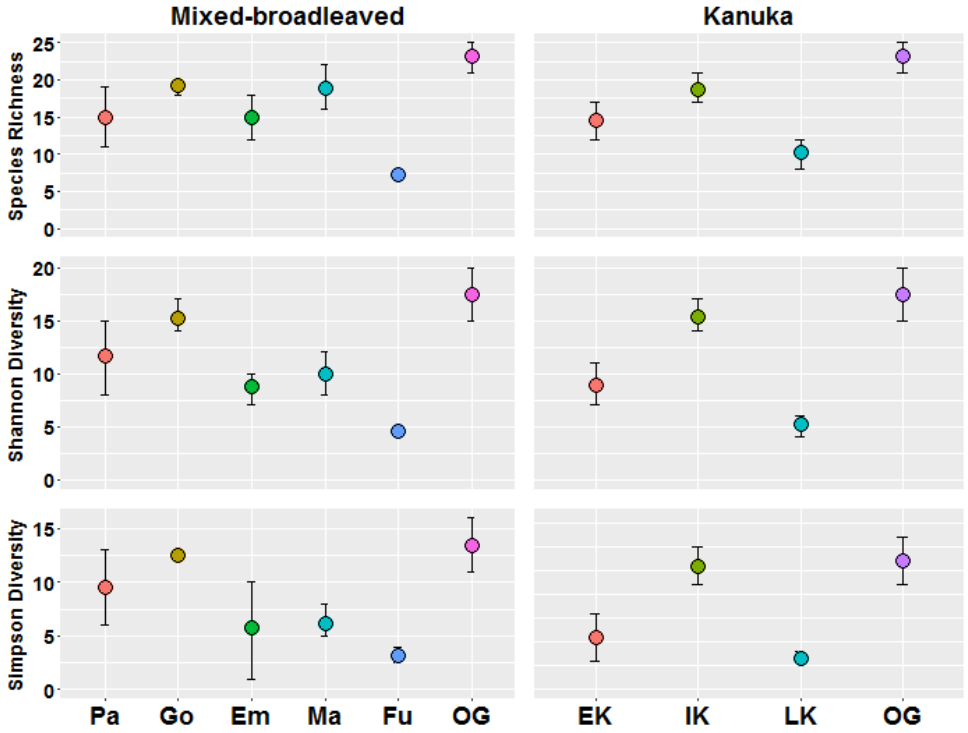


Figure 24. Mean ± 95 % CIs for the estimated beetle diversity attributes of each vegetation trajectory. See Table 23 for a numerical summary and a description of methods used. Non-overlapping CIs indicate a significant difference between means at the 5 % level (see Appendix in Chao et al. 2016). Pa = pasture,Go = gorse, Em = emergent natives, Ma = māhoe, Fu = fuchsia, OG = old growth (reference forest), Ek = early kānuka, IK = intermediate kānuka, LK = late kānuka.

Functional Groups

Most of the beetles encountered were herbivores feeding on plants or fungi (53 %), followed by predators (32 %) and the smallest fraction, mainly beetle larvae, were detritivores (14 %). The diversity of the latter group could not be compared between successional stages as too few individuals were encountered. The trends shown by the overall beetle diversity (Figure 24) were reflected in the herbivore guild, which is not surprising, as this group was the most abundant and speciose.

Predatory beetle patterns were difficult to assess along the mixed-broadleaved trajectory, due to the overlapping confidence intervals of the majority of the successional stages. The lowest predatory beetle richness was observed for the reference and māhoe forests. Māhoe and fuchsia forests were again distinctly different in their species richness. For the kānuka trajectory, all beetle predator diversity indices peaked at the late kānuka stage, while all other successional states, including the reference, contained lower values.

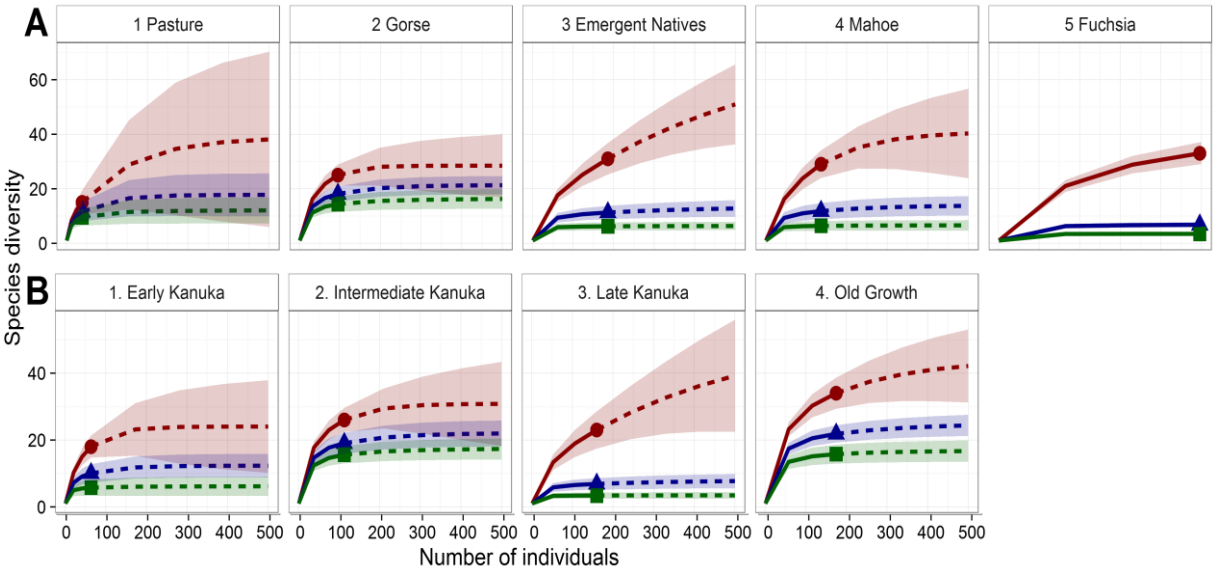


Figure 25. Beetle diversity profiles for successional stages along the two chronosequences: (A) mixed-broadleaved forest and (B) kānuka forest, also depicting the reference site (old growth) for both forest trajectories. Rarefied (solid line) and extrapolated (dashed line) curves denoting species richness (red), for Hill's Shannon (blue) and Simpson (green) indices for each successional stage. 95 % CIs (shaded areas) were obtained by bootstrapping (100 replications). The order of difference between the three curves gives an indication about community evenness, the larger the higher the dominance gradient. These curves also depict the sampling effort; no clear asymptote of a curve indicates a high number of species remained undetected.

Araneae

A total of 31 RTUs were recorded across all samples. Even pooled leaf litter samples contained low spider abundances, with less than 50 individuals per successional stage (Table 23). Nevertheless, sample coverage was still > 79 % for all successional stages even though estimated 95 % confidence levels were much broader than for the beetles.

For the mixed-broadleaved trajectory (Figure 26) spider richness and diversity displayed significantly higher values in the earlier successional stages (gorse, emergent natives) in comparison to the initial stage (pasture) and both older forest types (māhoe and fuchsia). Similarity to the reference forest could not be determined due to the large confidence intervals.

The kānuka trajectory again displayed a peak in mean diversity in the intermediate stage. All diversity indices were significantly lower in late kānuka in comparison to the two earlier development stages. The reference forest accommodated significantly higher spider richness and Shannon diversity than the late kānuka. However, it was statistically indifferent to the younger successional stages. The order of differences between Hill's numbers (Table 23) suggested once more a high level of species dominance in late kānuka and higher species evenness in intermediate kānuka.

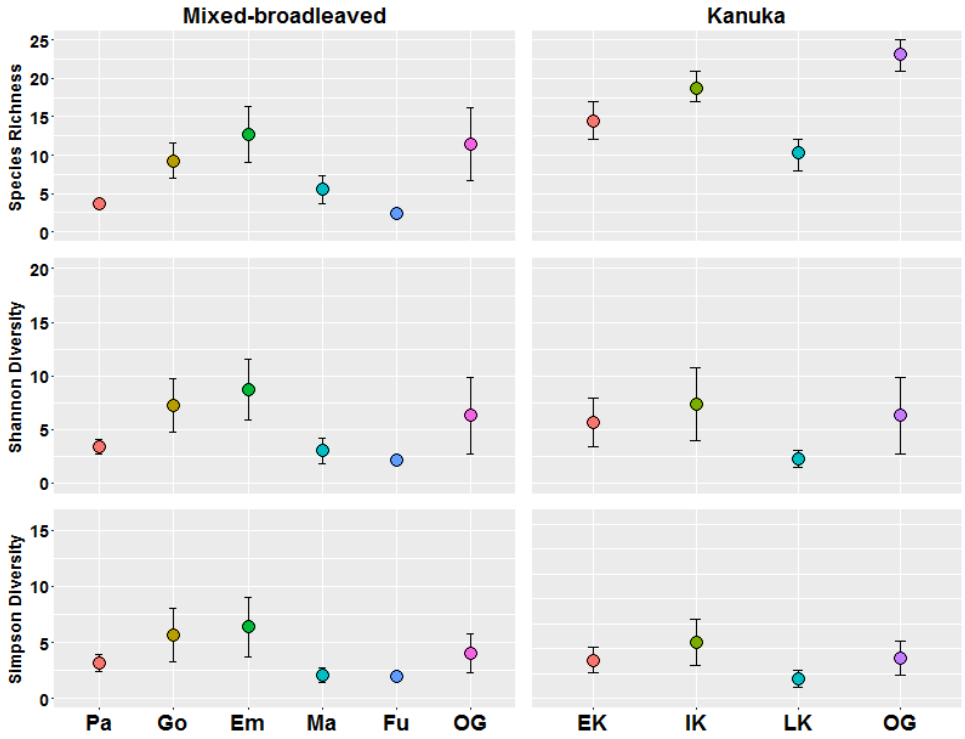


Figure 26. Mean ± 95 % CIs for the estimated spider diversity attributes of each vegetation trajectory (mixed-broadleaved and kānuka forest). Pa = pasture, Go = gorse, Em = emergent natives, Ma = māhoe, Fu = fuchsia, OG = old growth (reference forest), Ek = early kānuka, IK = intermediate kānuka, LK = late kānuka.

The Decomposer Group

The decomposer assemblage comprised earthworms (Oligochaeta), unspecified worms (Annelida), millipedes, amphipods (Amphipoda), slaters (Isopoda), and some adult and beetle larvae. Richness and diversity of the decomposers achieved an estimated sample coverage of at least 97 % for all vegetation types.

Within the mixed-broadleaved trajectory decomposer richness and diversity was significantly higher under gorse compared to all other stages including the reference forest. No statistical differences were found between any other successional stages (Table 24).

Early kānuka contained the highest decomposer richness within the kānuka trajectory (Table 24). The pattern displayed over progressing successional stage differed between both diversity indices. The reference site contained significantly lowest decomposer diversity (both indices) and richness. Similar to the mixed-broadleaved trajectory, values for species richness and Shannon/Simpsons indices differed widely, an indication that many species were scarce.

Table 24. Observed and estimated diversity of the decomposer functional group (across all taxa): species richness (N_0), Shannon (N_1) and Simpson (N_2) indices. Pooled abundances were used for each vegetation group; CI's were calculated using 100 bootstrapping replications. Estimated values were derived by interpolating all diversity measures to the lowest sample coverage estimation observed (0.97). n = absolute number of individuals observed, m = estimated number of individuals at a sample coverage of 0.97.

	Successional stage	n	N_0 obs.	SC	m	Estimated (mean, 95 % CI)		
						N_0	N_1	N_2
Mixed-Broadleaved	Pasture	265	11	0.98	164	8.4(6-11)	1.5(1-2)	1.2(1-1)
	Gorse	699	28	0.99	261	20(17-22)	5.6(5-6)	3.2(3-4)
	Em. Natives	868	22	0.99	127	10.1(9-11)	3.7(3-4)	2.4(2-3)
	Māhoe	509	18	0.99	151	12.2(11-14)	4(4-4)	2.4(2-3)
	Fuchsia	1422	22	0.99	148	10.4(9-11)	2.6(2-3)	1.6(2-2)
Kānuka	Early Kānuka	301	20	0.97	298	19.9(15-25)	5.1(4-6)	3.3(3-4)
	Int. Kānuka	304	16	0.99	101	12.7(11-14)	6.9(6-8)	4.6(4-5)
	Late Kānuka	655	17	0.99	125	11.5(10-13)	5.6(5-6)	4.2(4-5)
	Reference Forest	611	17	0.99	113	8.8(8-10)	3.3(3-4)	2.2(2-2)

Composition

Coleoptera

Overall compositional change

Beetle community composition differed significantly along the mixed-broadleaved trajectory (including the reference forest), according to PERMANOVA results (perm = 999) on abundance (*pseudo* $F_{(5,63)} = 2.04$, $R^2 = 0.14$, $p = 0.001$) as well as presence/absence data (*pseudo* $F_{(5,63)} = 2.6$, $R^2 = 0.17$, $p = 0.001$). Due to the comparable result, presence/absence data was not further explored. Pairwise comparisons showed that most successive vegetation stages had significantly distinct beetle compositions except gorse vs. emergent natives and māhoe vs. fuchsia ($p > 0.05$). Beetle composition of the reference forest differed significantly from all successional stages ($p < 0.01$). Gorse ($F_{(1,25)} = 1.9$, $R^2 = 0.07$, $p = 0.01$) and emergent natives (*pseudo* $F_{(1,26)} = 1.84$, $R^2 = 0.07$, $p < 0.01$) were most similar to the reference forest. Interestingly, Coleoptera composition was also similar between fuchsia, māhoe and the two later kānuka stages ($p > 0.05$), but the beetle community present in both broadleaved stages differed to that in early kānuka (*pseudo* $F_{(1,24)} = 1.8$, $R^2 = 0.11$, $p < 0.01$). Of the potential covariates and confounding variables (Table 21) investigated using step-wise-model selection (PERMANOVA), only canopy cover (*pseudo* $F_{(1,56)} = 1.87$, $p < 0.01$) and litter volume nested within successional stage (*pseudo* $F_{(1,56)} = 1.44$, $p < 0.01$) had a significant influence besides successional stage (*pseudo* $F_{(5,56)} = 1.84$, $p = 0.001$) itself, which displayed the strongest explanatory power ($R^2 = 0.12$) (Table

25). Still, all variables displayed a rather low overall effect on beetle composition ($R^2 < 0.15$).

Table 25. PERMANOVA results for differences in beetle composition along the mixed-broadleaved trajectory (successional stages) in relation to canopy cover (%), fresh litter volume (cm^3), and the interaction of litter volume and successional stage. This table represents the final result based on 999 permutations and Bray-Curtis dissimilarities, after step-wise mode selection using all variables listed in Table 21.

	SS	MS	Df	F	R^2	P
Litter volume	0.3254	0.32541	1	0.9118	0.012	0.591
Vegetation group	3.2876	0.65753	5	1.8424	0.120	0.001
Canopy cover	0.6692	0.66923	1	1.8752	0.024	0.008
Litter volume x Veg	2.5724	0.51447	5	1.4415	0.094	0.004
Residuals	19.9859	0.35689	56		0.730	
Total	27.371	68	68			

For the kānuka trajectory, beetle composition changed significantly along the successional stages, for both abundance (*pseudo* $F_{(3,43)} = 1.46$, $R^2 = 0.09$, $p < 0.05$) and presence/absence data (*pseudo* $F_{(3,43)} = 2.0$, $R^2 = 0.12$, $p < 0.01$), hence only abundance data was further analysed. PERMANOVA showed no significant differences between the three kānuka stages, but each of these groups differed significantly to the reference forest (early kānuka: $F_{(1,25)} = 1.87$, $R^2 = 0.07$, $p = 0.01$; intermediate kānuka: *pseudo* $F_{(1,24)} = 1.69$, $R^2 = 0.07$ $p < 0.05$; late kānuka: *pseudo* $F_{(1,27)} = 1.88$, $R^2 = 0.07$, $p < 0.01$). Step-wise model selection (PERMANOVA) including all potential covariates and confounding variables showed that regeneration density had a weak but significant effect on beetle composition. Even though successional stage displayed double the effect size of regeneration density, it was insignificant due large within group variance (Table 26).

Table 26. Final PERMANOVA results for attributes influencing beetle composition over the kānuka trajectory. Step-wise model reduction was carried out on a full model including all variables listed in Table 21. Df = degrees of freedom; SS = sum of squares; MS = mean sum of squares; *pseudo* F = F value based on 999 permutation.

	SS	MS	Df	F	R^2	P
Regeneration density	0.6315	0.63153	1	1.5965	0.033	0.029
Vegetation group	1.4687	0.48956	3	1.2376	0.077	0.099
Residuals	16.6144	0.39558	42			
Total	19.0013		46			

The overall effect of successional stage on beetle composition (R^2/F) was very low in both vegetation trajectories. There was also high within-group variance, with

an average distance to the group median being between 0.55 and 0.59 for all successional stages. PERMANOVA is known to be prone to mistake differences in within group variances for between group variances. Even though the within group variances were not significantly different from each other, they were still rather large. NMDS ordinations (Figure 27) further confirmed this, as within group variances were so high that no separation between the different successional stages could be seen based on beetle composition.

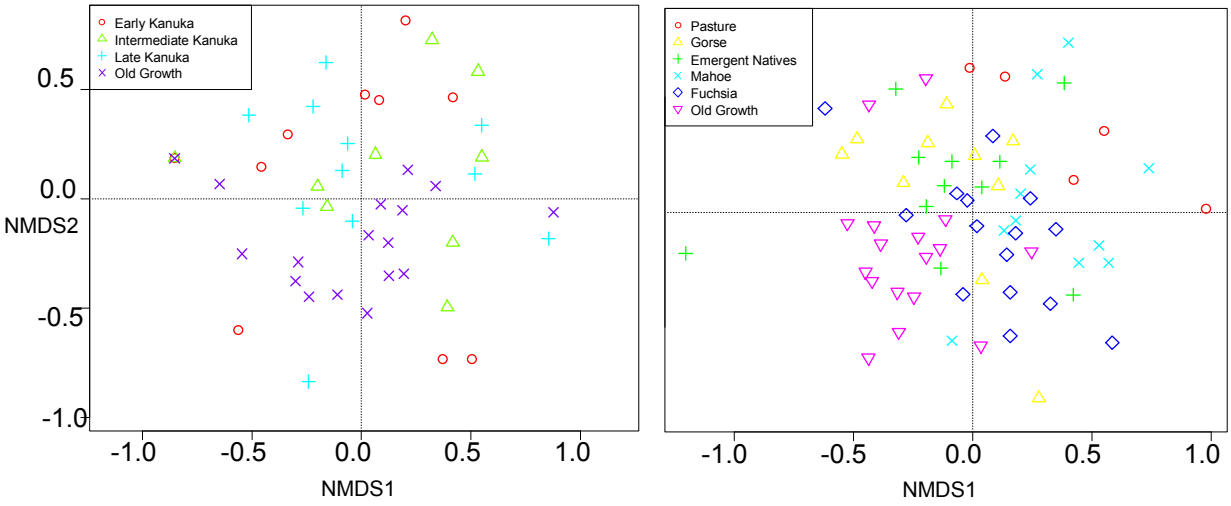


Figure 27. NMDS plots based on Bray–Curtis similarities for the beetle communities in the kānuka (stress: 0.26) and the mixed-broadleaved (stress: 0.28) trajectories. Even though for both ordinations convergent solutions were found, plant successional stages were not well represented by the beetle communities.

Coleoptera functional groups

Compositional differences of functional groups were investigated using PERMANOVAs on raw, untransformed data.

No significant differences in predator composition were found between successional stages for the mixed-broadleaved trajectory (*pseudo* $F_{(5,14)} = 1.08$, $p > 0.2$, perm = 999) and covariate/confounders had no significant effect ($p > 0.1$). For the kānuka trajectory, no significant effect of successional stage on predator composition was observed (*pseudo* $F_{(2,7)} = 1.4$, $p > 0.1$, perm = 999), only leaf litter moisture displayed a weak influence on community assemblage (*pseudo* $F_{(1,7)} = 2.2$, $R^2 = 0.18$, $p < 0.05$, perm = 999) in a PERMANOVA including both variables. No predatory beetle was encountered in early kānuka. After correcting for altitude, herbivore composition differed significantly between successional stages, but with a low effect size along the mixed-broadleaved (*pseudo* $F_{(5,59)} = 1.6$, $R^2 = 0.11$, $p = 0.001$, perm = 999) and kānuka trajectories (*pseudo* $F_{(3,38)} = 1.5$, $R^2 = 0.10$, $p < 0.01$, perm = 999).

For the decomposers, within group multivariate variation differed significantly (betadisper) for both trajectories, which contained only seven (kānuka) and nine (mixed-broadleaved) species ($p = 0.5$). Log transformed data (log+1) established homogenous variances between groups in both cases. However, successional stage had no significant effect on decomposer composition in all vegetation sequences ($p > 0.05$).

Araneae

Even though only singletons and doubletons were removed before analysis, only eight spiders were left in the data set (see Table 23 for an overview of single/double occurrences of species). No significant compositional differences were reported for the mixed-broadleaved (*pseudo* $F_{(4,32)} = 1.1$, $p = 0.34$) or kānuka trajectory (*pseudo* $F_{(3,31)} = 0.7$, $p = 0.8$). Log transformation of the spider abundances produced a similar, non-significant result. Neither covariates nor confounder variables showed a significant effect on spider composition (intermediate kānuka: *pseudo* $F_{(1,11)} = 1.8$, $p = 0.09$; old growth = *pseudo* $F_{(1,11)} = 2.1$, $p = 0.07$; fuchsia = *pseudo* $F_{(1,7)} = 2.1$, $p = 0.07$).

Millipedes

No significant difference in millipede composition was found by a PERMANOVA between successional stages of the kānuka trajectory (*pseudo* $F_{(3,31)} = 0.9$, $p = 0.6$). A weak but significant difference in community composition was observed for the mixed-broadleaved trajectory (*pseudo* $F_{(5,55)} = 1.7$, $R^2 = 0.13$, $p = 0.005$). Subsequent pairwise comparisons did not show significant differences between successional stages. None of the tested confounder or covariates (intermediate kānuka: *pseudo* $F_{(1,10)} = 0.5$, $p = 0.8$; old growth = *pseudo* $F_{(1,15} = 1.1$, $p = 0.34$; fuchsia = *pseudo* $F_{(1,17)} = 2.1$, $p = 0.24$), had a significant effect on millipede composition.

The Decomposer Group

Amphipoda (61 %) and slaters (10 %) were the most abundant taxa within the decomposer group. Probably due to site conditions, there was a large variation in individuals encountered per sample, especially of amphipods (Amphipoda). Species data was therefore reduced to presence/absence for the PERMANOVA procedure in an attempt to offset the effect of site conditions. Decomposer composition displayed a weak but significant difference along the mixed-broadleaved (*pseudo* $F_{(5,63)} = 1.7$, $R^2 = 13$, $p < 0.05$) as well as the kānuka trajectory (*pseudo* $F_{(3,46)} = 3.2$, $R^2 = 17$, $p < 0.001$), both included the reference

forest. Pairwise comparisons for the mixed-broadleaved trajectory, displayed significant differences only between the reference forest and pasture ($F_{(1,62)} = 3$, adj. $p < 0.01$, perm = 999).

For the kānuka trajectory, decomposer composition differed significantly ($p > 0.05$) between most successional stages except early vs. intermediate and late kānuka vs. reference forest. Dissimilarity was greatest between early and late kānuka ($F_{(1,45)} = 5.1$, adjust. $p < 0.01$) and between early kānuka and reference forest ($F_{(1,45)} = 7.3$, adjust. $p < 0.01$). NMDS ordinations for both forest trajectories had intermediate stress levels (< 0.30) and found convergent solutions. Still, these ordinations did not differentiate well between successional stages along either trajectory (Appendix 16), reflecting the rather low overall effect size reported by the PERMANOVA.

6.5.2. Ecosystem Function

Soil

Soil attributes largely displayed the expected trends with progressing succession (see Figure 28). However, large between plot variations in these variables (insufficient sampling), impeded the detection of significant differences between successional stages.

Soil organic matter (SOM) accumulation did not differ significantly along the two vegetation trajectories (i.e. organic carbon). Organic matter quality (C:N) improved along the mixed-broadleaved but not the kānuka trajectory. Generally, the lower the C:N ratio the higher the nitrogen availability for plants, hence the better the SOM quality. The C:N ratio was significantly lower for all successional stages in both vegetation trajectories in comparison to the reference forest ($p < 0.001$), indicating low-quality SOM at the reference site. The increasing dominance of broadleaved species in both trajectories was reflected by a significant change in pH-values ($p < 0.01$). With the exemption of gorse, the reference forest possessed the lowest mean pH ($p < 0.05$) in contrast to all successional stages in both trajectories. As microbial activity is positively associated with increasing pH, it is not surprising that it displayed a similar pattern and is highly correlated (Table 27).

Total nitrogen (N) was not significantly different between successional stages along the kānuka trajectory, including the reference forest ($p = 0.8$). For the

mixed-broadleaved trajectory, no significant differences ($p > 0.05$) were observed between gorse and the mixed-broadleaved forest stage (māhoe and fuchsia). The post-hoc Games Howell test indicated significantly higher soil N for the mixed-broadleaved successional stage than under all kānuka stages (overall Welch's ANOVA: $F_{(5,18)} = 6.4$, $p < 0.001$) and the reference forest ($p < 0.05$). N values for gorse were indifferent to all other successional stages along both vegetation trajectories.

Total Olsen P varied significantly across all successional stages along both vegetation trajectories ($F_{(5,17)} = 3.4$, $p < 0.0.5$). Highest levels were observed under gorse (36 mg kg^{-1}) and the combined mixed-broadleaved forest stages (18.3 mg kg^{-1}). Due to a large within-successional-stage variation in P values, only the difference between reference forest and the mixed-broadleaved forest stage were significant ($p < 0.05$). Measured soil variables were often strongly correlated for example, pH positively and C:N ratio negatively with microbial activity (Table 27).

Table 27. Spearman's rank correlation coefficients (r_s) between soil variables for the mixed-broadleaved and kānuka trajectories, including the reference forest. Holm corrected p-values for multiple comparisons are displayed.

	Soil variables	pH		Organic C (%)		Total N (%)		C / N		Mineralisable-N		Olsen P (mg/kg)	
		r_s	p-value	r_s	p-value	r_s	p-value	r_s	p-value	r_s	p-value	r_s	p-value
Broadleaved forest	pH			-0.19	0.89	0.27	0.69	**-0.65**	<0.001	**0.54**	0.03	0.37	0.31
	Organic C (%)	-0.19	0.34			**0.78**	<0.001	-0.03	0.89	0.49	0.06	0.20	0.89
	Total N (%)	0.27	0.17	**0.78**	<0.001			**-0.54**	0.03	**0.67**	<0.001	**0.61**	0.01
	C / N	**-0.65**	<0.001	-0.03	0.89	**-0.54**	<0.001			**-0.50**	0.05	**-0.70**	<0.001
	Mineralisable-N	**0.54**	<0.001	**0.49**	0.01	**0.67**	<0.001	**-0.50**	0.01			0.33	0.41
	Olsen P (mg/kg)	**0.37**	0.05	0.20	0.30	**0.61**	<0.001	**-0.70**	<0.001	0.33	0.08		
Kānuka forest	pH			-0.37	0.42	-0.05	1.00	-0.47	0.09	**0.78**	<0.001	**0.50**	0.05
	Organic C (%)	**-0.37**	0.05			**0.80**	<0.001	0.24	1.00	-0.02	1.00	0.10	1.00
	Total N (%)	-0.05	0.80	**0.80**	<0.001			-0.26	1.00	0.30	0.87	0.26	1.00
	C / N	**-0.47**	0.01	0.24	0.20	-0.26	0.16			**-0.54**	0.03	-0.26	1.00
	Mineralisable-N	**0.78**	<0.001	-0.02	0.92	0.30	0.11	**-0.54**	<0.001			0.44	0.15
	Olsen P (mg/kg)	**0.50**	<0.001	0.10	0.60	0.26	0.17	-0.26	0.17	**0.44**	0.02		

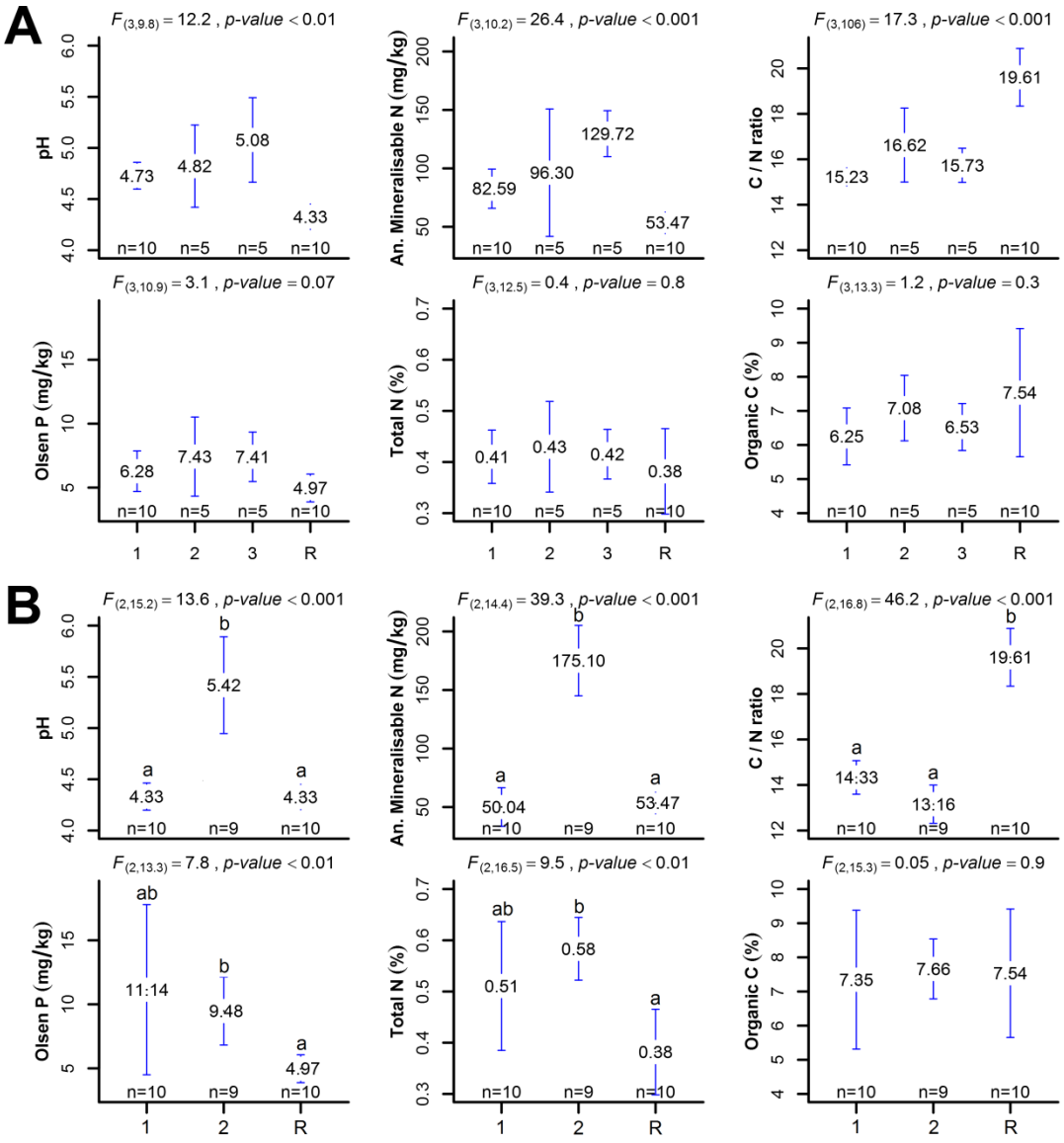


Figure 28. Mean ± 95% CI for all measured soil variables by successional stage for the kānuka (A) and mixed-broadleaved trajectories (B). Successional stages are abbreviated in (A): 1 = early kānuka, 2 = intermediate kānuka, 3 = late kānuka, R = reference forest; in (B): 1 = gorse, 2 = mixed-broadleaved forest (māhoe and fuchsia), R = reference forest. *F* - and *p* - values indicate results of Welch's ANOVA, testing for the overall effect of successional stage. Same letters above successional stages indicate non-significant differences ($p > 0.05$) from the post-hoc Games Howell test. Anaerobic mineralisable N was log transformed to achieve normality for the ANOVA but mean ± CI values are displayed untransformed.

Leaf Litter Decomposition

Does decomposition change during progressing plant succession?

Of the 3 g initially installed in the leaf litter bags, the smallest remaining weight after 18 months was observed under fuchsia (0.26 g) and the largest in early kānuka (2.0 g). After accounting for confounding variables: slope and altitude, recovery time displayed a weak (24 % of the variance explained) but significant effect ($p < 0.01$) on total leaf litter weight loss over the mixed-broadleaved trajectory (Table 28). Fuchsia and māhoe sampling plots were combined to

increase statistical power; the reference forest was omitted. For the kānuka trajectory, this trend was even less distinct, with time accounting only for 15 % of the variance within leaf litter decomposition rates (adj. $R^2 = 0.11$, $F_{(1,31)} = 4.8$, $p < 0.05$). To depict the within group variability and to get an indication of the general trend, mean weight loss (as a proxy for decomposition) was also inspected on the successional stage level (Figure 29). Leaf litter decomposition seemed to increase with progressing successional stage in the kānuka trajectory, whereas trends seem to be more dynamic in the mixed-broadleaved trajectory.

Table 28. Multiple regression analysis for the mixed-broadleaved trajectory, of the relationship of recovery time with total leaf litter decomposition rates (% loss) adjusted for slope and altitude (overall model result: adjusted $R^2 = 0.24$, $F_{(3,45)} = 4.5$, $p = 0.006$).

	Coef.	Std. Error	*t* value	*p*-value
Time	0.23	0.074	3.166	0.002
Slope (°)	-0.20	0.074	-2.773	0.008
Altitude (m)	-0.04	0.024	-1.783	0.08

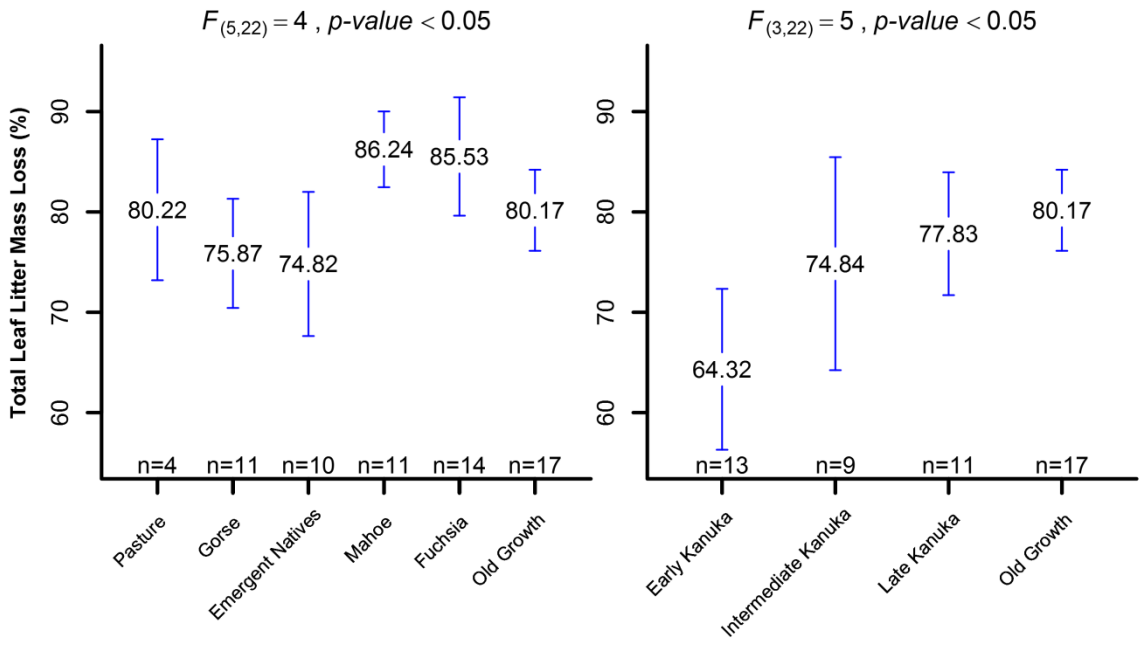


Figure 29. Relative dry leaf litter mass loss after 18 months for the mixed-broadleaved and kānuka trajectories. Mean ± 95 % CIs and sample sizes (n) are shown separately for each successional stage. F and p values are derived from Welch's ANOVA.

Is there a measurable link between the decomposer group and leaf litter decomposition?

Linear models did not detect a significant relationship between leaf litter decomposition and composition or abundances of the functional group of decomposers for the mixed-broadleaved trajectory ($p > 0.5$). Only a weak but significant effect for decomposer abundances on litter decomposition was observed for the kānuka trajectory ($R^2 = 0.13$, $F_{(1,31)} = 4.7$, $p < 0.05$). Interestingly, decomposer abundances (log10+1 transformed) did not differ between successional stages (kānuka: $F_{(3,22.3)} = 0.4$, $p = 0.7$; mixed-broadleaved trajectory: $F_{(5,23.5)} = 1.8$, $p = 0.13$).

6.6. *Discussion*

Leaf Litter Invertebrates

Beetles

Beetles were the most diverse of all taxa extracted from litter samples (RTUs = 72), a result shared by others (Meloni & Varanda 2015). No pronounced pattern for beetle diversity was observed moving along the mixed-broadleaved forest trajectory. The two alternative later successional stages (māhoe and fuchsia) displayed contrary trends. However, mean values indicate that diversity might peak at an early stage (gorse), subsequently decreasing over progressing successional time. The reference forest displayed consistently, if not always significantly, higher diversity values for all three diversity measures than the earlier successional stages. For the kānuka trajectory, diversity initially increased from the early to mid-successional stages and then dropped sharply, and remained lower than the reference forest.

Hopp et al. (2010), is the only other study (as far as the author is aware) to look explicitly at the response of leaf litter beetles during forest regeneration on abandoned land with widely varying disturbance level (e.g. logged, grazed). They used a chronosequence approach to investigate changes in beetle assemblages over increasing recovery time on two soil types in second growth forests in Southern Brazil. The dominant beetle families observed in Southern Brazil were concurrent with the findings of this study: Staphylinidae (36 %) and Curculionidae (21 %). Hopp et al. (2010) detected a consistent trend over increasing recovery time for overall beetle richness on one soil type (cambisol), but not on the other (gleysol). On gleysol, overall species as well as single family richness peaked at an early stage and then dropped again. This result is similar

to what the current study demonstrated for the kānuka and indicated for the mixed-broadleaved trajectory. Overall species richness was similar to the old growth forest after 35 - 50 years for the cambisol. Beetle richness at the family level was observed by Hopp et al. to reflect the overall trend but displayed much higher variation. Ottermanns et al. (2011) provide some additional information about vegetation development along the same cambisol chronosequence employed by Hopp et al. (2010), in an attempt to link vegetation structures to leaf litter beetle composition. The findings of Ottermanns et al. suggest that even though vegetation composition becomes more similar over time towards the reference sites, the intermediate successional stages are still distinctly dissimilar to it. Structural measures such as dbh and canopy cover showed a higher convergence and might have caused the similarity of beetle richness after 35 - 50 years on this soil type. Neither Hopp et al. (2010) nor Ottermanns et al. (2011) provided more information about the forest successional stages in terms of similarity of plant composition and relative progress along the successional pathway on the gleysol soil type.

Other studies, that have investigated beetle responses to restoration over time have used different sampling technique (e.g. pitfall traps) that favour capture of different beetle families and results are therefore not as directly comparable. In one example, species richness of ground beetle fauna of Matiu-Somes Island (Wellington Harbour, New Zealand) was found to increase over time since reforestation, reaching highest values in a site established in 1900 (Watts & Gibbs 2002). Watts and Gibbs suggest that this result might be driven by differences in canopy cover, litter mass, canopy height and deadwood.

Restoration plantings on former pasture sites at Kennedy's Bush (*Port Hills,* New Zealand) also reported an increase over time in beetle richness, with highest values present in an old growth forest (Reay & Norton 1999). Reay and Norton also suggested that vegetation structure was the underlying cause of this.

There is some evidence that beetle diversity seems to be driven by changes in vegetation structure influencing in turn environmental conditions (e.g. temperature, moisture, nutrients) (e.g. Ottermanns et al. 2011; Reay & Norton 1999; Watts & Gibbs 2002). The study at Hinewai used pooled data for each successional stage, thus introducing a high variability for vegetation structure and microsite conditions. This might have obscured the underlying trends especially along the mixed-broadleaved trajectory. However, the difference

between reference sites and successional stages along the two trajectories was still apparent.

Of key importance to the objectives of this study was the finding that the observed vegetation successional gradient was only weakly reflected in beetle assemblage structure for the mixed-broadleaved trajectory and not at all for the kānuka sequence; although all vegetation stages did differ slightly relative to the old growth forest. Hopp et al. (2010) also reported weak differences between assemblages along successional stages, whereby litter volume seemed to have a larger effect than vegetation stage. In Hinewai, litter volume also had a significant, but weaker effect than successional stage. Reay and Norton (1999) also failed to find a strong pattern in assemblage differences between sites. Only the reference site and the youngest restoration planting, which was still mainly covered in exotic grass, were compositionally distinct to the other, intermediate restoration plantings within the Matiu-Somes Island study (Watts & Gibbs 2002). It seems difficult to untangle what is driving the overall beetle composition, which in addition is a very heterogeneous group with a broad range of habitat preferences and functional roles. Time since recovery, that is, successional vegetation stage seem to be not the main driver.

In summary, litter/ ground beetle diversity seems to be influenced by small-scale changes in vegetation structure and composition, while beetle composition appears to be only marginally affected. From a restoration success perspective, diversity indices are not overly informative, as it remains unknown in which species habitats differ. Furthermore, early successional habitat can hold the same species diversity as reference sites. They also seem to be difficult to predict, as the driving factors are not completely understood and act at a small-scale. Beetle composition also did not change in a predictive manner and the relationship with vegetation recovery was very weak. Neither diversity nor an overall compositional approach seems to be informative for the assessment of restoration success for litter beetles, and their recovery is difficult to predict and does not necessarily follow patterns of vegetation succession.

Spiders

Low abundances of spiders were observed in this study, as has been noted by others (e.g. Mallis & Hurd 2005). A clear trend was observed for spider richness, peaking in early to mid-successional stages of both forest trajectories. The reference site did not hold higher spider richness than the earlier vegetation stages. Interestingly, spider richness followed the same pattern as beetles for the

kānuka forest, but not for the mixed-broadleaved trajectory. Some studies report that spider richness is positively connected to heterogeneous habitat or later successional stages (Ryndock et al. 2012; Uetz 1990; Willett 2001). Litter depth and volume, nutrient content, and litter structural complexity in particular have been highlighted as habitat factors which may be important drivers of litter spiders diversity (Bultman & Uetz 1982; Mawson 1986; Simmonds et al. 1994). Uetz also noticed that the factors influencing spider richness and abundances might also change with season (Uetz 1979). However, other studies have found it difficult to link spiders to habitat measures and reported that their diversity did not increase over vegetation succession (Aitchison & Sutherland 2000; Hurd & Fagan 1992; Mallis & Hurd 2005). No obvious connections to litter (volume, moisture) or vegetation characteristics (canopy cover, deadwood) could be seen in this study. Otherwise, late kānuka, with its relatively high litter volume and moisture, and the reference forest, with the highest deadwood content and the lowest canopy cover, could justifiably have been expected to have held much higher species richness. Noticeably, with the exception of pasture, forest types possessing low spider richness all contained a high amount of broadleaved cover, which led to a high soil pH. Soil pH has been shown to influence prey composition and abundances of spiders (Loranger et al. 2001; Van Straalen & Verhoef 1997).

Spider composition did not differ significantly between successional stages in Hinewai. It has been suggested that spider assemblages might not undergo succession as such and that it is difficult to predict their composition, as most species are rare and associated with (largely) unknown specific resources (Mallis & Hurd 2005). It is therefore not surprising that others assessing restoration success report only a weak dissimilarity between spider communities and no change of spider diversity over progressing recovery time (Reay & Norton 1999). However, Simmonds et al. (1994) observed a similar pattern for spider richness to this study. Richness displayed a peak in 7 - 18 year old restoration plantings and was comparatively lower in their old growth forest sites.

The Decomposer Group

Total decomposer richness was highest in early successional stages (gorse and early kānuka), reaching almost twice the number of species as the reference site. It is not clear which habitat components were responsible for this result, as measured variables such as litter volume/moisture and soil attributes, were not similar in both vegetation types. Late kānuka forest exhibited lower richness

than the reference, while the mixed-broadleaved trajectory was again displaying an ambiguous trend.

In summary, none of the observed invertebrate diversity measures followed trends in vegetation successional development in a consistent, predictable way. Moreover, species assemblages changed only weakly or not at all over increasing recovery time for both forest trajectories. There may be a number of reasons for this result:

(i) The large variation in microsite conditions within successional stages, which were often larger than between vegetation stages. Small-scale differences in moisture, litter volume and temperature have frequently been emphasized to influence invertebrate abundances and with that diversity (Bultman & Uetz 1982; Koivula et al. 1999; Ottermanns et al. 2011; Ziesche & Roth 2008). As it was necessary to pool invertebrate samples for plots within each successional stage these variables could not be integrated into the diversity analysis, and hence they might have concealed the underlying pattern. Even though these variables have been included (and corrected for) in the compositional analyses, still only weak patterns were observed. The chronosequence approach could have contributed to the large variation in microsite conditions; hence, this method might be not entirely suitable for studying leaf litter invertebrates.

(ii) Low number of individuals in samples, especially for spiders. Even though according to entomologists a good time of year was chosen for sampling (pers. comm. Chris Green and Peter Johns), it might have been not ideal in that particular year.

(iii) In contrast to species richness and diversity indices, rare species are often excluded from compositional analysis (as done here) and less abundant species get in addition less weight (Bray-Curtis distance here). It might be that abundant invertebrate species (often generalists) are not good discriminators between successional stages. The true difference might be in the presence and absence of rare species, specialised on specific habitat requirements such as deadwood.

As a result of these underlying complexities, it was difficult to determine if the inconsistent trends observed were caused by the chronosequence approach, (ecologically unsuitable groupings) or if they are indeed an inherent characteristic of leaf litter invertebrates in the research area. Many studies use a

higher level approach to study meso- or macrofauna, such as overall RTU or order/group richness and composition (Jansen 1997; Nakamura et al. 2003) as well as total group abundances (Didham et al. 2009). Total RTU richness across all taxonomic groups (as opposed to looking at beetles and spiders separately) was not tested here, as preliminary analysis conducted on the full dataset that did include all taxa together was found to hold low information content and results were even harder to interpret. Invertebrate abundances are linked to microsite conditions, and therefore only meaningful if used in habitats showing no large variation in small-scale conditions; hence, abundances were not investigated on their own.

Some studies have successfully focused on specific taxonomic groups and identified invertebrates to species level within these to determine diversity and compositional differences between vegetation groups (R. J. Harris et al. 2004), the level of disturbance (Willett 2001) or restoration success (Wodika et al. 2014). This approach, which is contrary to the current study using RTUs, can produce easier to interpret results with a much higher information content (e.g. native vs adventive species, generalist vs specialist), but it requires a specialist and a well-researched taxonomy and ecology of species. If these conditions are met, a compositional approach focusing on specific taxonomic groups or species might be superior to a diversity based procedure.

Soil and Litter Decomposition

The behaviour of soil variables over time was generally observed as anticipated based on the vegetation successional development. The expected increase in soil organic matter was somehow concealed by a high variation in total organic C within successional stages. Organic matter quality as well as microbial activity increased over successional time. This might be the result of higher quality litter input, due to the growing dominance of broadleaved species in both trajectories (P. Wardle 2002). All soil measures were highly variable within successional stages, again a likely result of small-scale differences. Organic matter, even though similar in quantity, was of lower quality under the old growth forest. Soil under beech and kānuka forest contained relatively low nitrogen levels, which is a common characteristic of soils in New Zealand (P. Wardle 2002). Together with the high C:N ratio, this might indicate that nitrogen is a limiting factor for plant growth and microbial activity in the beech forest. Somewhat, unexpectedly N values for gorse did not differ largely to all other successional stages along both vegetation trajectories (probably due to a high sample variance). Even though

gorse is a nitrogen-fixer, around 40 % of the nitrogen remains immobilized in the shrub and only gets released into the soil once the shrub dies (Egunjobi 1971a, 1971b). Hence, the higher amount of N observed within the mixed-broadleaved stage might be caused by the release of nitrogen previously fixed within gorse after its dieback.

Available phosphate was highest in the mixed-broadleaved trajectory indicating a higher level of anthropogenic influence in comparison to the kānuka forests. High variation in total P, especially within the gorse group, suggested prolonged effects of known past management actions; fertilisation (higher P values) and top-soil removal for areas which inherit low P values (5 mg kg^{-1}). Phosphate level seemed to be lowest in the reference forest. The low levels of P observed in soils under the reference forest, are typical for older forests in New Zealand, which become more P-limited over time (R. B. Miller 1968; Stevenson 2004). It has been hypothesised that spread of the main tree species in the old growth forest (red beech, *Fuscospora fusca*) could be limited by an absence of certain mycorrhizal fungi in the surrounding areas (Dickie et al. 2012; Leathwick 1998). Other studies have found relationships between high soil fertility and absence of mycorrhiza (Chu-Chou & Grace 1987; Gerschefske et al. 1988). Hence, the question arises whether the relatively high nutrient levels (P, C:N ratio) observed for the mixed-broadleaved forests (māhoe and fuchsia) could play a part in this issue.

The extent to which microbial activity and invertebrate communities account for litter decomposition differs between ecosystems and seem to be influenced by climatic conditions (Wall et al. 2008). Microbial activity increased over successional time as did leaf litter decomposition in both trajectories. The trend displayed by the pH followed exactly the same pattern, limiting (lower) or favouring microbial activity (higher). Microbial mass in acid soils is often dominated by fungi, which are generally slower in processing detritus than bacteria, which in contrast, are more important in nutrient richer, higher pH soils (Bardgett & Wardle 2010).

The overall trend for litter decomposition was rather weak due to a high within group variation. Other studies (Borders et al. 2006; S. C. Ward et al. 1991) found no difference between different aged restored forest and reference forests, which might have been a result of similar vegetation composition. Ward et al. (1991) noticed strong trends between decomposition rates, moisture and understorey cover. In other words, decomposition relates to a range of micro/macro scale site

factors such as environmental conditions, litter quantity, and quality as well as the decomposer community (Couteaux et al. 1995). If there is large within-group variation in these conditions, they might obscure the general pattern.

The reference forest behaved somewhat unexpectedly; it retained one of the lowest pH-values, low microbial activity, did not possess higher decomposer richness or a different composition compared to other successional stages, and yet exhibited relatively high leaf litter decomposition. The reason for this might be related to decomposition bags having being filled with red beech leaves. Plant litter quality is known to be a major driver of decomposer composition and diversity (D. A. Wardle et al. 2006). Wardle et. al. (2006) showed that bags filled with litter from various species, mixed and unmixed, resulted in colonisation by different decomposer communities under the same forest type. Recently, a leaf litter study in a *Nothofagus* mixed forest in Argentina found that plants might promote decomposer communities that favour mineralisation of their own litter (Vivanco & Austin 2008). The same conclusion is shared by a number of experimental studies (e.g. StricklandLauberet al. 2009). Specialisation of decomposers on 'home' leaf litter has been suggested but has not been tested for *Nothofagus* species in New Zealand (Ayres et al. 2009). However, results of this study support the suggestion that soil biota in infertile communities (red beech forest) might be better adapted for decomposing litter of low quality than soil biota in fertile communities (mixed-broadleaved forest, gorse) (StricklandOsburnet al. 2009). If this is the case, relative decomposition for the other groups could have been underestimated in relation to the reference site.

A link between decomposer faunal community and leaf litter decomposition was not readily apparent in this study. This is not necessarily surprising, as more research under real field conditions is necessary to establish and understand feedback loops between the two (Bardgett & Wardle 2010). Moreover, Wardle et al. (2006) demonstrated that the identity of the major species supplying the leaf litter had strong effects on faunal density and composition, with some degree of specialisation within the decomposers. Hence, samples in a very close proximity of each other, but taken under different plant species, may hold different invertebrate assemblages. It might be, therefore, that the successional stages based on vegetation criteria are too broad to extract any sensible patterns for litter macro- and mesoinvertebrates that act on much finer spatial scales. Hence, these measures seem to be not particularly helpful for assessing restoration success in forests.

6.7. *Summary*

Assessment of restoration success is largely based on vegetation parameters. In particular, biodiversity offsets have to assess and model the impact on site biodiversity as well as its anticipated recovery. By far the largest proportion of biodiversity is located below ground and yet is mostly ignored. This chapter investigated if belowground measures of biodiversity change in a similar fashion to vegetation over two main successional sequences. The role of leaf litter invertebrates in the decomposition processes was assessed to see if a link was readily measurable. Trends in leaf litter invertebrate composition and diversity did not show a consistently strong relationship with plant successional development. Patterns were inherently difficult to interpret and in most cases did not correlate well with habitat variables. It remains uncertain if this was caused by some part of the study design or if it is an inherent characteristic of litter assemblages. However, chronosequences are often the only way to assess progress in restoration projects, due to a lack of long-term data. Easier to obtain soil measures directly relating to the nutrient cycle provided more straightforward and easier to interpret results. Anaerobic mineralisable nitrogen correlated well with the measured leaf litter decomposition. It proved to be a less time-consuming approach than the litter bag method and relates directly to decomposer activity.

The inclusion of leaf litter invertebrate biodiversity might be most meaningful as a measure of restoration success if focusing on absence and presence of key taxa with either essential ecological functions or which have inherent biodiversity value because they are found nowhere else (e.g. old growth specialists involved in the decomposition of coarse woody debris). To achieve this however, specialist taxonomic and ecological knowledge is required and such expertise is increasingly hard to find. In the absence of expert skills, it may not be feasible to assess accurately the condition of the belowground fauna and thus, resources may be better focused on easier to obtain measures of ecosystem function like anaerobe mineralisable nitrogen and soil C:N ratio.

Chapter 7
Conclusions

7.1. *Abstract*

This thesis investigated which ecosystem attributes are most suitable for assessing and predicting restoration success in forests, especially in biodiversity offset situations. Attributes frequently used or suggested for evaluation of restoration success were identified through an intensive literature review in Chapter 3. They were scored according to their measurability, information content, and well-known characteristics. These attributes belong to three broad groups: ecosystem composition, ecosystem structure, and ecosystem function. To verify the findings of the literature review, suitability of these attributes was then tested in a restoration project (Hinewai Reserve). A space-for-time substitution (chronosequence) methodology was applied to compare the recovery of these ecosystem characteristics from pasture back to forest. Two main vegetation trajectories were investigated: (1) kānuka (*Kunzea robusta*) and (2) mixed-broadleaved forest with its two subtypes being either dominated by (2a) māhoe (*Melicytus ramiflorus*) or (2b) fuchsia (*Fuchsia excorticata).* This chapter now summarizes the findings for vegetation, invertebrate, and soil related attributes. Predictability, recovery speed, and information content of these attributes are evaluated. Results of this study are compared with outcomes from other research. A key set of attributes that seem to be generally applicable in forest ecosystems is presented. Even though biodiversity offsets aim to achieve an overall no net loss of biodiversity at a site (BBOP 2013), recovery of the below ground biota which usually embraces the highest proportion of ecosystem diversity is often overlooked (D. A. Wardle 2002). This thesis, therefore, investigated the connection between vegetation recovery and belowground ecosystem aspects. Restoration success in the research system is finally evaluated and a hypothetical biodiversity offset example is used to describe challenges surrounding attribute selection for offsets. Limitations of this study are identified and opportunities for further research highlighted. Finally, conclusions based on thesis and literature results are presented and general recommendations are given for developing an objective framework for attribute selection in forests.

7.2. *Attribute Suitability for Assessing and Predicting Restoration Success*

The ultimate goal of biodiversity offset models is to predict future restoration success and the time frames associated with achieving this at an offset site in relation to a reference system. To take the time lag between biodiversity loss at the impact site and restoration success at the offset project into account, area multipliers are used to adapt the offset ratio (Bull et al. 2013). Hence, time frames estimated to reach restoration success are crucial as they can significantly influence offset size (Moilanen et al. 2009). Table 29 shows how large the effect of attribute selection can potentially be. Listed attributes display considerable variation in convergence to the reference system, and with that, the accomplishment of restoration success. For this reason, attribute choice should not be taken lightly. Behaviour of most ecosystem attributes identified in Chapter 3 (Table 3), with the exception of landscape factors, was tested in Hinewai (see Table 29 for a complete list of tested attributes). Attribute description and their use in other studies are discussed in Chapter 2. An extensive discussion of individual attribute performance at Hinewai reserve can be found in Chapters 3-6. In this chapter, an overall summary of their general suitability with respect to biodiversity offset application in forests is provided.

Table 29. Convergence of the oldest second growth forests along the two investigated trajectories towards the reference site. Values are given as a mean percentage for each vegetation and soil chemical ecosystem attributes tested in preceding chapters of this thesis. CWD = coarse woody debris, dbh = diameter at breast height (1.4 m). For functional indices only results for the canopy layer is displayed.

Thesis Chapter			Attributes	% of reference value	
				Late Kānuka	Broadleaved forest (Māhoe/Fuchsia)
Structure (4.)			Canopy cover (%)	59	111
			Gini index	113	110
			Shannon index	89	92
			Vertical diversity index	120	110
			Basal area (m^2 ha^{-1})	76	74
			Stem density (stems ha^{-1} >5cm dbh)	323	224
			Canopy height (m)	50	31
			Mean dbh (cm)	36	35
			Sdbh (cm)	42	38
			Snags volume (m^3 ha^{-1})	38	3
			Mean dbh snags (cm)	64	16
			CWD volume (m^3 ha^{-1})	28	4
			Mean dbh CWD (cm)	57	62
Composition	Composition (3.)		Dissimilarity ferns	14	8/6
			Dissimilarity woody species (IV)	3	2/1
			Saplings of late success. species (count ha^{-1} dbh1-5 cm)	21-64	0/0
			Seedlings of late success. species (count ha^{-1} dbh<1 cm)	1-3	0/0-1
			Trees of late success. Species (count ha^{-1} dbh>5 cm)	10-50	0/3-30
	Biodiversity (5.)	Functional	Functional richness index	160	40/130
			Functional divergence index	112	80/93
			Rao's quadratic entropy index	550	100/300
			Functional dispersion index	414	129/300
			Functional evenness index	178	140/138
			Posteriori functional group richness index	237	159/212
			Functional group proportion (e.g. dispersal)	-	-
		Traditional	Rarefied species richness (tree tier)	264	209/277
			Rarefied species richness (shrubs tier)	186	108/130
			Shannon diversity index	202	166/233
			Inverse Simpson diversity index	173	156/225
			Simpson's evenness index	458	416/83
		Taxon.	Average tax. diversity index	283	317/318
			Taxonomic distinctness index	180	176/173
			Variation in tax. Distinctness index	450	368/364
			Average tax. distinctness index	172	165/106
Function (6.)			pH-value	117	125
			Olsen P (mg kg^{-1})	149	190
			Total organic carbon (%)	86	101
			Total nitrogen (%)	110	152
			C:N ratio	80	67
			anaerobic mineralisable nitrogen (mg kg^{-1})	242	327
			Leaf litter decomposition (total leaf mass loss %)	97	108/106

7.2.1. Predictability of Attribute Behaviour and Scores

The uncertainty surrounding offsets is often caused by the technical difficulties in predicting restoration outcomes, e.g. attribute scores and related time frames (Maron et al. 2016; Norton 2009a). An important related question is which ecosystem attributes follow a consistent trajectory over recovery time and display a moderate to strong trend i.e. are predictable. To test the ability to predict future attribute values, trend strength, and directionality over increasing recovery time or successional stage was assessed (Table 30). Linear models were applied for univariate attributes and PERMANOVA models were used for multivariate attributes.

The strongest, unidirectional trends were observed for vegetation structural measures (e.g. canopy height, basal area) and all plant species diversity indices. Some of the structural attributes such as stem density and canopy cover showed differences in trend direction over the two successional trajectories. This is not surprising and is mainly a result of the successional differences between the chronosequences. One trajectory is still in its pioneer phase (kānuka) in transition to an intermediate successional stage, whereas the other one (mixed-broadleaved forest) has already passed the pioneer phase and is now in its structural building stage.

These findings are consistent with Suganum and Durigan (2015) who also reported that canopy cover, basal area, density, and species richness were the most predictable attributes for assessing restoration success in riparian tropical forests. A similar result was obtained by Lebrija-Trejos et al. (2010) for tropical dry forests in Mexico. The latter study found that overall stem density, basal area, species richness, and the Shannon index showed a strong trend over increasing recovery time. Their results also further support the findings of this study (Chapter 5), that structural data assessed at the species group level can aid better understanding of the underlying successional dynamics. Overall, the results of this thesis and the studies described above as well as others (Chazdon et al. 2007; Goosem et al. 2016; Guariguata 2001) all suggest that diversity and vegetation structural attributes are often deterministic processes following a consistent trajectory with successional time.

Compositional attributes measured by analysing species similarity matrixes of plant and invertebrate species in Hinewai displayed only weak to moderate trends over recovery time. Similar results have been frequently reported in the

literature (Goosem et al. 2016; Guariguata 2001; Hopp et al. 2010; Reay & Norton 1999; Suganuma & Durigan 2015) leading to the general conclusion that compositional trends can be difficult to predict. Reasons are that both deterministic (e.g. environmental conditions) and stochastic processes (e.g. arrival order of species) can determine species composition (sensu Temperton & Hobbs 2004). Species composition in particular is difficult to forecast in restoration projects because anthropogenic influence affects environmental site conditions introducing new or changed filters to species establishment (e.g. nutrient enriched soil favours a certain set of species) (Nuttle et al. 2004; P. S. White & Jentsch 2004).

An alternative compositional approach is to investigate presence or abundances of specific species, species groups or functional groups (McCune & Grace 2002). The species-specific approach was evaluated using the example of late successional tree species in Hinewai. Unfortunately, due to the low numbers of red beech (*Fuscospora fusca*) and thin-barked tōtara (*Podocarpus laetus*) observed, trends along successional trajectories could not be assessed statically; hence, this approach appeared unpredictable in Hinewai. However, proportions of functional groups present in a vegetation type based on dispersal, life form (i.e. shrubs, trees), and successional group (i.e. early, late successional) were found to be generally predictable in the research area. Again, due to the virtual absence of late successional tree species, no trend was observed for this specific functional group over recovery time. To some extent, this may be a result of this attribute being generally unpredictable, but it is more likely that it highlights a restoration issue in Hinewai Reserve: arrested restoration (e.g. Cramer et al. 2008). The low regeneration success of late successional tree species indicates underlying dispersal, establishment, or survival issues causing either slow progress along the successional trajectory or changing their endpoint. Results of studies conducted mainly in tropical forests, also suggest that the proportion of certain functional traits in a community over recovery time can be predicted. Such traits comprised shade tolerance and wood density (Dent et al. 2013; Plourde et al. 2015; Suganuma & Durigan 2015) both related to late successional trees, and seed/fruit size and dispersal modes (Liebsch et al. 2008; Lohbeck et al. 2012; Suganuma & Durigan 2015) reflecting dispersal limitations.

All ecosystem attributes that were found to react in an unpredictable way over increasing recovery time can be roughly sorted into three groups, which are discussed below:

(i) *Attributes that are highly sensitive to small-scale site differences, (e.g. leaf litter volume and regeneration densities*). Suganuma and Durigan (2015) advocated that regeneration density, especially for saplings (1-5cm dbh) can be reliably predicted and is thus a good indicator for restoration success. Contrary to this finding, regeneration density acted unpredictably in Hinewai. Regeneration density is known to be sensitive to a wide range of factors working at different spatial scales, which can impede accurate measurement and prediction of trends (Grubb 1977; Hanson et al. 2011; Hessenmoeller et al. 2013). This is especially true in chronosequences, where it is difficult to keep small-scale site conditions similar between plots. In Hinewai, a large variation in seedling and sapling densities occurred due to small-scale differences in site conditions. The chronosequence study by Suganuma and Durigan (2015) covered an even more diverse set of site conditions, including a wide range of different soil types, climates, disturbance levels, planted tree species, and stem densities. Although the exact drivers are not clear, given the high degree of spatial variability present in their study, it is surprising these two studies resulted in differing predictions.

(ii) *Attributes which gain increasing importance in later successional stages.* Unsurprisingly, indicators of later successional stages such as larger amounts of deadwood (Spies & Franklin 1988) were virtually absent from the early to intermediate successional stages investigated (except for remains of harvested stems) in this study. Vesk et al. (2008) estimated that at least 150 years would be needed to establish levels of coarse woody debris comparable with old growth forests at revegetated sites in central Victoria, Australia.

(iii) *Attributes where the underlying cause is uncertain, such as taxonomic and functional indices*. Taxonomic and functional diversity indices have often been recommended for assessing restoration success but have rarely been tested. At Hinewai, taxonomic indices produced weak to strong trends over increasing recovery time and results varied between the two vegetation trajectories. The author is not aware of any published study comparing taxonomic diversity indices for restoration purposes. No or weak to strong trends were observed for functional diversity indices, but strength of trends differed widely between vegetation trajectories for Hinewai Reserve. Audino et al. (2014) and Derhé et al. (2016) investigated dung beetles (Coleoptera: *Scarabaeinae*) to evaluate restoration progress in tropical forests and found either no or weak trends for most of the indices over increasing recovery time, while trend direction differed

between both studies for some indices. Similarly, in Mexico a study following a vegetation successional gradient from fallow towards forest Lohbeck et al. (2012) found no or weak trends in functional diversity indices with increasing recovery time. Derhé et al. (2016) suggest that the relationship between recovery time and functional diversity indices might be context dependent, being heavily dependent on the traits selected and indices used. All of these observations are supported by the results of this thesis which also found that they can be difficult to interpret.

Some attributes could not be exclusively assessed in this thesis due to financial constraints. For example, soil attributes were only measured for a subset of plots (50 out of 105 plots). Even though soil attributes seemed to behave in a predictable way, this was difficult to prove statistically due to a high variance in the data. For example, the expected increase in soil organic matter was somehow concealed by a high variation in total organic C within successional stages. However, organic matter qualities, as well as microbial activity, seemed to enhance over successional time in Hinewai. Available mineral nutrients and the amount of soil organic matter often show clear temporal trends (Odum 1969), being also strongly correlated with vegetation development (Alday et al. 2012; Du et al. 2007; Zak et al. 1990). As was found in Hinewai, microbial biomass and activity have previously been found to show increasing trends over recovery time in other restoration projects (sensu discussion in J. A. Harris 2003). However, predictability was not explicitly assessed in these studies and methods used varied between projects. As far as the author is aware, the method used in Hinewai (anaerobic mineralisable nitrogen) was not used in other restoration studies. Further research, including a meta-analysis of the published literature is necessary to assess predictability of soil attributes over recovery time.

Table 30. Summary of results from preceding chapters on predictability of selected vegetation and soil chemical attributes in Hinewai Reserve. See in text discussion as to why some of the attributes appear to be unpredictable, but might actually point towards certain restoration issues at the reserve.

Predictability	Description of attribute behaviour	Chapter 3 **Vegetation composition**	Chapter 4 **Plant biodiversity**	Chapter 5 **Vegetation structural**	Chapter 6 **Function**
Predictable with single trend direction	Strong and consistent trends in all trajectories for the same species groups. (Model R^2>50)		species richness species diversity indices	canopy height structural diversity indices vertical diversity index basal area mean dbh sdbh	
Predictable with different trend directions	Moderate to strong trends, direction of trend differs between trajectories(model R^2>25)		functional group measures (i.e. dispersal mode, life form)	stem density canopy cover	
Potentially difficult to predict	Attribute showed a moderate trend, prediction accuracy depends on the time frame (model R^2>25)	compositional trends over time (PERMANOVA)			
Unpredictable	No, weak or inconsistent trends within all or one of the trajectories. (model R^2<25)	size class structure of certain species groups (e.g. late successional) assemblage similarity to reference	taxonomic diversity indices functional diversity indices	leaf litter volume regeneration density all deadwood measures	leaf litter decomposition
Difficult to assess	Too few incidences to examine predictability or to different from the reference site, or sample				Soil chemical properties (C,N,P, pH) Microbial activity

7.2.2. Information Content

Predictability is an important characteristic of ecosystem attributes for offset models. However, equally or even more important appears to be the information the attribute is contributing towards the estimation of restoration success. The determination of when restoration has been successful is dependent on the project objectives. In the case of biodiversity offsets, this will be how much the restoration site converges to the reference system. This reference system is most likely to be a natural second growth or old growth forest suffering some level of degradation. This thesis investigated if any attributes could be identified that could be almost universally meaningful for assessing forest condition, and with that, restoration success.

Tree related structural attributes, in particular canopy height, canopy cover, basal area, the mean dbh, and its standard deviation proved good descriptors of structural development. These attributes are easy to measure and to interpret and relate well to successional development of forests. These basic measures were determined to be universal suitable attributes, as every forest will undergo successional developments described by them.

Compositional measures revealed most about potential restoration issues i.e. absence of late successional tree species for Hinewai reserve. Similarity matrices (ordination methods, PERMANOVA) can be very useful tools to assess convergence over time to the reference forest (Reay & Norton 1999; sensu Ruiz-Jaén & Aide 2005a). They displayed a steady progress along the two vegetation successional pathways. However, these measures did not show much convergence towards the reference site over time. Similarity indices were unable to identify the underlying cause of this. A similar finding lead Suganuma and Durigan (2015) to dismiss compositional measures for restoration success assessment, reasoning that they are unpredictable and take a long time to recover.

Even though ordinations are most frequently used to assess species composition in restoration, this is not the only approach available (Ruiz-Jaén & Aide 2005a). Some authors propose that focusing on abundances or presence of selected species, species groups (Leighton Reid 2015) or functional guilds (Brancalion & Holl 2016) might be more useful. This is supported here where the attributes with the highest information content for Hinewai were the presence of certain species groups i.e. late successional tree species. The low abundances of these

species helped to establish the inherent difference to the reference system and highlighted restoration issues. A similar observation was made by Suganuma and Durigan (2015) who found changes in slow growing or shade resistant species ecologically meaningful and predictable for the assessment of restoration success. However, they reasoned that these measures rely on labour intensive botanical identification and could not be influenced by restoration actions. Consequently, they did not include them in their final set of attributes suitable for describing restoration success in tropical forests. Instead, they advocated the use of tree species richness in the understorey (saplings), using a recognisable taxonomic units approach. The authors suggested that a diverse layer of saplings indicates that potential environmental filters have been overcome and might act as an indicator of ecosystem stability. The Hinewai study found species diversity and richness measures some of the least meaningful attributes. This discrepancy emphasizes the context depended assessment of attribute suitability. The forests present at Hinewai can be regarded as species-poor in respect to tropical forests. If a second growth forest is richer in species than the old growth forest used as a benchmark, how does that relate to the assessment of ecosystem condition? Higher species richness in this case, is likely to be related to the effect of past disturbances, with increasing resource availability (Catford et al. 2012) favouring generalist and pioneer plants (Tabarelli et al. 2012). Hence, it is doubtful if species diversity measures for vegetation are at all suitable for assessing restoration success, at least in species-poor ecosystems. Species identity and with that guild membership (specialist, late successional species) seems to be of much more importance in these systems. For species-rich systems, measurable trait data could be used to establish group affiliation without identification of species identity (Brancalion & Holl 2016).

Attributes describing soil development, such as nutrients, pH, or microbial activity, are useful especially when assessed in conjunction with other measures. They can help to detect barriers to restoration and aid interpretation of changes in compositional attributes. However, they might be most useful as a one off measurement at the beginning of a project, to identify restoration barriers; soil attribute development (topsoil) is generally strongly related to vegetation succession and does depend on the degree of soil degradation that has occurred in the past (Alday et al. 2012; Du et al. 2007; Zak et al. 1990).

Least useful in this study were attributes related to vertical and horizontal layering (e.g. Gini index) in forests. All measures tested showed no meaningful

convergence to the reference sites (see Chapter 5). Assessing horizontal forest complexity by analysing canopy cover based on aerial images might be more useful, but needs further testing (Dickinson et al. 2016) and may be less suitable in a closed-canopy mesic forest environment such as that studied here. Functional diversity and taxonomic indices were generally hard to interpret and did not add more information towards ecosystem condition. Some of the more readily interpretable taxonomic indices were furthermore correlated to traditional species diversity indices.
In summary, any form of information aggregation into an index seems to lead to a high loss of information and is therefore often difficult to interpret. Indices seem to be not very useful for assessing restoration success for offsets at least in relatively species poor temperate regions of the world.

7.2.3. Recovery Speed

Structural attributes recovered fastest in Hinewai, but results varied between measures (Table 29). This is not surprising as structural features are typically connected to specific successional stages. Canopy closure is usually associated with early stages (stand initiation), whereas formation of larger sized trees, which is accompanied by an increase in larger dimensions of deadwood, is linked with later successional stages (Guariguata 2001; Spies 1998). Deadwood volume can be high initially but decline over time as a result of stumps and crowns remaining on-site after harvesting (as in Hinewai). Compositional attributes are generally regarded to be the last to establish – which was true for Hinewai Reserve. It has been suggested that it can take between 100 to 1000 years to reestablish vegetation composition (Curran et al. 2014).

Generally, recovery speed of attributes is a double-edged sword for biodiversity offsets. Some attributes (like larger dimensions of deadwood /habitat trees) will develop eventually. It might take a long time, but as soon as a forest is established, it will inevitably happen. In these cases, the uncertainty surrounding these attributes is low. This applies to most of the structural attributes, which will most likely converge over time towards the reference values as the forest ages. On the other hand, forest composition, which also can take a long time to recover, might never converge to the reference site and might be thus connected to a high uncertainty. These forests might develop into so-called novel ecosystems, harbouring a species composition adapted to the altered site conditions created by past management actions (Hobbs et al. 2006, 2009,

2013). Re-creation of compositional attributes must therefore be seen as key variables in offsets to achieve a no net loss.

7.2.4. A General Set of Attributes

What kind of attributes will be almost universally useful and should be included in offsets models in situations involving forest ecosystems?

Structural attribute development is predictable and can be ecologically meaningful; hence, these attributes should be included in offset models. They can also link well to other components such as function or faunal species composition in the ecosystem (Ferris & Humphrey 1999; Franklin et al. 2002; McElhinny et al. 2005; Young 2000). Exact response shapes over time are likely to differ for structural attributes between forest ecosystems and depend on successional time frames observed, hence a sound knowledge of these parameters for the specific forest types is essential (see Delang & Li 2013 for a discussion). Development of structural attributes over succession is for many forests well described, hence trend direction and strength should be feasible to forecast within time frames of restoration projects from an offset perspective. However, as already mentioned, development of structural features is closely linked to forest successional stages. Hence, attributes need to be selected according to the successional stage of the reference site.

Compositional measures are the most meaningful attributes as they can be sensitive to the management applied such as the exclusion of browsing animals (D. A. Wardle et al. 2001). They could therefore be used explicitly to demonstrate the additionality (i.e. improvement of ecosystem condition would not have happened without the restoration action) which is required by offsets (ten Kate et al. 2004). Then again, they can be difficult to predict and might take a long time to recover. Some authors suggest they are therefore generally less suitable to assess restoration success (Durigan & Suganuma 2015; Suganuma & Durigan 2015). Notwithstanding this, in the case of biodiversity offsets, which specifically aim at a no net loss of biodiversity, compositional measures have to be included in some form in order to assess if the restoration site will indeed converge towards the reference condition. If convergence is uncertain, which is usually coupled with a long time frame of recovery, biodiversity offset is likely to be unsuitable for this specific forest.

A recent meta-analysis comparing 108 restoration projects found that active restoration methods such as planting can enhance predictability and speed of

community composition recovery greatly (Curran et al. 2014). Many factors can potentially influence species establishment such as distance to seed source or germination requirements, which can be bypassed through actively introducing the species of interest. This might be especially true for larger sized highly disturbed areas, which might recover very slowly or never converge to reference systems at all, but instead develop into novel ecosystems (Hobbs et al. 2006, 2009, 2013).

Similarity matrices in combination with abundances or presence of specific species groups of interest (e.g. late successional species, rare species) should be included in offset models at least for the canopy layer. In addition, all structural attributes mentioned above can be assessed for each species of interest individually. For species-rich forest such as tropical and subtropical forests, a functional approach relying on easily measurable traits could be more appropriate than focusing on species identity due to practical constraints (labour intensive botanical identification or species not described) (Brancalion & Holl 2016). The author is, however, unaware of studies relying only on measured trait data to assess restoration success. Hence, future research should focus on the identification of traits that are most meaningful and easy to obtain for these purposes.

In conclusion, a list of attributes that can be almost universally applied in biodiversity offset situations comprising forests is suggested in Table 31. This table depicts only the basic list of attributes, and additional attributes relevant to the specific project objectives and forest type should be selected individually.

7.3. *Relationship between Vegetation Recovery and other Species Groups*

Most biodiversity offsets models are based on measures of vegetation (Gonçalves et al. 2015). Indeed all attributes recommended above focus on vegetation, specifically trees, given they represent the distinctive element of a forest. The inherent advantage of vegetation attributes is that they are generally easy to obtain, and show less seasonal variation than faunal measures. Their surrogacy value for other aspects of the ecosystem, such as fauna and function, is mostly assumed rather than tested (Hilderbrand et al. 2005; Suding 2011). Recent studies caution that vegetation measures do not necessarily reflect the recovery of faunal groups at a site (Cristescu et al. 2013; Hanford et al. 2017; Kwok et al. 2011).

Table 31. Summary of vegetation and soil chemical attributes suggested being almost universally applicable and meaningful for biodiversity offsets in forests.

	Ecosystem Attributes		
	Recommended	**Project specific**	**More research needed**
Structure	* Mean dbh * Standard deviation of tree dbh * Tree height (canopy height) * Canopy cover * Basal area * Stem density		* Vertical / horizontal structural complexity * Functional diversity indices * Taxonomic diversity indices
Function		* Nutrient pools direct (chem. properties) * Soil organic matter (total SOM stock or C:N)	* Soil microbial biomass/activity
Composition	* Similarity matrices to assess overall trends (Ordination, PERMANOVA) * Abundances (in different size classes) / presence of specific functional groups or species and species groups of interest (e.g. climax, exotic or rare species) in different layers (i.e. canopy, understorey)	* Species diversity / richness	* Abundances / presence of functional groups based on relatively easy to measure traits without identification to species level

In particular, recovery of invertebrate communities seems to not link well to the restoration of vegetation (Oliver et al. 2014). To test this assumption leaf litter invertebrate recovery was evaluated for Hinewai. Leaf litter and topsoil layers represent functional and diversity hotspots in forest ecosystems, often representing the largest part of biodiversity in a forest (Ballantine & Schneider 2009; D. A. Wardle 2002). This thesis however, could not establish an association between recovery of vegetation and leaf litter invertebrates. This result is similar to that from other studies, especially for spiders (Aitchison & Sutherland 2000; Hurd & Fagan 1992; Mallis & Hurd 2005) and leaf litter beetles (Hopp et al. 2010).

A number of reasons could be responsible for this result, such as chronosequences being unsuitable for assessing processes that are affected by small-scale habitat conditions, or the influence of conditions that are varying independent of site age (e.g. mice abundance). Yet, the result could also be genuine, caused by the limited dispersal abilities of invertebrates preventing them from recolonising the surrounding areas in the same speed as vegetation. More in-depth research is necessary to investigate the effect of restoration on

litter or soil invertebrates. In the light of the current knowledge gap for community and individual leaf litter and soil invertebrate behaviour, their diversity and the additional taxonomical challenges they pose, these invertebrates are not recommended here as an appropriate species group for assessing forest biodiversity offsets. A way to bypass these difficulties would be to focus on well described and meaningful key taxa as practised in Australia (D. F. Ward & Larivière 2004). However, further research in most parts of the world will be needed to identify these taxa and verify their suitability.

The surrogacy value of vegetation for fauna cannot be generally assumed in case of biodiversity offsets, which try to provide measurable and transparent assessments of site biodiversity. Specific measures should rather be included in offsets only for particular known species or functional groups of interest.

7.4. *Restoration Success at Hinewai Reserve under a Theoretical Offset Example*

Restoration is regarded to be successful if the specified restoration objectives are achieved. The restoration goal at Hinewai was to permit natural succession to unfold by removal of impediments to natural succession such as grazing pressure (Wilson 1994). By this definition, the restoration project has been successful as successional processes are taking place at all sites in the research area. If, however, the restoration objective would have been to recreate a system similar to the old growth forest present, the outcome would be different and is explored over the next few paragraphs.

To evaluate attribute choice for offsets further, a hypothetical biodiversity offset has been created for Hinewai Reserve. The hypothetical offset proposes that an energy company had built a wind farm in 1987 at one of the old growth sites and the research area was used as an offset site. As site conditions were estimated to be favourable for natural succession and seed sources are in close proximity, minimum interference management was chosen at the offset site (the current management at Hinewai). The designer of the offset estimated that in 50 years all vegetation will be in a very clear trajectory back to the reference site as suggested by Wilson (1994) – restoration will be successful. Now, 25 years later, the progress of the restoration towards the reference is assessed.

Structural attributes such as canopy cover, basal area, canopy height and mean diameter indicate that both second growth forests are slowly progressing towards

the old growth forest (Table 29). Basal area showed a greater convergence than mean diameter and its standard deviation. Characteristic structural elements of mature forests such as larger sizes of dead wood are still missing. It is evident that it will take much longer than 50 years for most attributes to reach reference values. However, as trends are strong and directional, based on structural attributes, restoration seems to be progressing successfully, even though the associated time lag has been underestimated and resulted in too low an offset ratio.

In contrast to this, the compositional attributes indicate that both second growth forests are still a long way from reaching the reference forest condition (similarity matrices). To further investigate why the forests are still so dissimilar to the reference, certain species groups can be examined in more detail. Firstly, the apparent lack of late successional tree species is prominent. One forest (kānuka) has some late successional trees present in different size classes and might be in transition to the reference. In the other forest (mixed-broadleaved), virtually no late successional trees are present and the time frame until this forest converges to the reference is uncertain. Therefore, succession can be seen as arrested. Soil attributes and functional groups can be used to assess the cause of the arrest. These attributes indicate that the absence of late successional species is most likely to be a mixture of a nutrient enriched soil promoting the generalist broadleaved species and dispersal limitations of the old growth forest species. However, as there is only a limited pool of late successional tree species, it is very likely that these will establish eventually, despite the time frame being unclear.

This above example highlights the importance of inclusion of compositional measures into biodiversity offset. It is evident that it will take a very long time until the characteristic species composition will, if ever, develop. Even though this could be accelerated by planting the late successional tree species, other key elements of mature forests, such as large dimensions of deadwood and presence of large trees, cannot be forced. Hence, this study further supports the conclusion of other authors that re-creation of old growth forests by reforestation is generally inappropriate for biodiversity offsets due to the large time frames and associated uncertainties involved (Curran et al. 2014; Gibbons et al. 2016; F. Quétier et al. 2015; Spake et al. 2015). If the theoretical impact site would have been not the old growth forest but the oldest regenerating second growth present at Hinewai – species composition and structural development could be restored

within 40 – 100 years under passive management, and substantially faster through restoration plantings. Thus, it seems much more feasible to model and predict earlier successional stages for offsets using reforestation techniques.

Another issue with offset models is that attributes progress at different rates towards the reference value, with that influencing the calculated time lag and with that the offset size. This will pose the largest issues when mature (or old growth) forests are used as a reference. For example, canopy cover can converge in under 20 years towards the old growth site (kānuka), whereas mean stem diameter did not even converge after 120 years. Which attribute should now be included in an offset model? As closed canopy is the first attribute to establish in regenerating forest, it would be one of the earliest goals to achieve in a restoration site. However, to appropriately estimate the time lag until the forest can be seen as ecologically restored, mean diameter and its range, being an indicator of a forest maturity (and consequently structural complexity) (Franklin et al. 2002) would be much more appropriate. Hence, it is yet another signal that the destruction of old growth forests can generally not be counterbalanced by reforestation offsets. In order to estimate the suitable time lag until a forest is ecologically of similar value as the one present at the impact site, ecosystem attributes that might potentially take a long time to recover seem to be the most meaningful, hence should be considered in an offset model.

7.5. *Limitations of this Study and Future Research Needs*

Even though attributes were tested and compared along three different vegetation trajectories, this thesis represents just one case study. Furthermore, as no long-time data set was available, a chronosequence approach was used to assess the recovery of the different ecosystem attributes. Even though the time frames observed are relatively long (70 - 120 years) they do not cover the life cycle of some of the dominant broadleaved species such as māhoe or fuchsia, nor that of the late successional species (> 500 years). Later successional stages are therefore not included in the analyses, giving an incomplete picture of successional processes at Hinewai Reserve. However, the focus of this study was not on successional processes *per se* but rather on the recovery of certain ecosystem attributes in time frames of restoration projects. The chronosequence approach might also be not entirely suitable for studying species groups such as leaf litter invertebrates and ecosystem processes like leaf litter decomposition, which are influenced by small-scale site conditions. To attenuate this issue,

relative trends rather than absolute differences in attribute values were investigated. For these reasons, further studies are recommended to test the suitability of the attributes suggested.

This thesis was not able to answer all questions relating to attributes suitable for biodiversity offsetting. Some attributes such as functional group or functional diversity measures, as well as taxonomic indices, require much more testing in other restoration settings. For example, how do we assign functional groups without full taxonomic information for restoration assessment in species-rich forests? Is a functional approach at all suitable for species-poor forests? Is anaerobic mineralisable nitrogen a valid indicator for microbial activity in other ecosystems? Do leaf litter invertebrate groups relate better to vegetation development if long-term monitoring data is used?

7.6. *Summary*

The overall objective of this thesis was to aid the procedure of developing objective biodiversity offsets for forests by investigating general ecosystem attribute suitability as input variables in the associated offset models. This research identified a set of ecosystem attributes mainly comprising structural and compositional variables, which are suggested to be ecologically meaningful, measurable and, if used appropriately, behave predictably (Table 31). Especially combining structural attributes with compositional components (e.g. basal area per species) can preserve higher information content for evaluating future restoration success than assessing attributes across all species. These general attributes have to be complimented by variables describing forest type and site-specific characteristics, which have to be carefully selected for each specific project.

Ecosystem attributes typically recover at different rates. In order to appropriately estimate offset associated time lags, slow recovering attributes should not be dismissed for offset models but should receive special attention. Species of interest should be assessed directly rather than assuming that habitat re-creation might act as a proxy unless there is a strong empirical support for this assumption. It is also important to recognise the different successional stages of forests, which are generally related to the establishment of different structures and processes (e.g. early succession = canopy closure, high stem density; late succession = large sized trees). Hence, attributes should be chosen depending on the specific successional stage of the reference forest.

Finally, one of the most ambiguous concepts in biodiversity offsets was coined by Salzman and Ruhl (2000). They suggested that selected ecosystem attributes should capture foremost 'what we care about' in biodiversity (DOC 2014; S. Walker et al. 2009). In New Zealand, where Hinewai Reserve is located, this rather subjective approach is commonly applied for biodiversity offsets. New Zealand offsets are currently applied on a voluntary basis, but plans are under way to make them a more integral part of impact assessment on public conservation land (DOC 2014). The ambiguous concept of 'what we care about' could be resolved by using a standardised scoring method based on an ecosystem benchmark catalogue for forests. This concept is applied by several other countries and has the advantages of accelerating the assessment process and offering more predictable and repeatable outcomes (Fabien Quétier & Lavorel 2011). A catalogue listing important ecosystem components per forest type (e.g. red beech forest, lowland/upland podocarp-broadleaved forest) and related attribute value ranges could be used to provide standardized benchmark values, ideally per successional stage. The general applicable attributes suggested here, could be used as a framework, supplemented by attributes describing the characteristics of the particular forest type. Scorecards for ecosystem attributes could then be used to assess status and trend of site biodiversity objectively. Further testing and building on the recommendations provided herein will eventually lead to a more robust, objective and meaningful system for biodiversity offsetting in forest ecosystems.

Bibliography

Addison JA, Trofymow JA, Marshall VG (2003) Abundance, species diversity, and community structure of Collembola in successional coastal temperate forests on Vancouver Island, Canada. Applied Soil Ecology 24 : 233–246

Aide TM, Zimmerman JK, Pascarella JB, Rivera L, Marcano-Vega H (2000) Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. Restoration Ecology 8 : 328–338

Aitchison CW, Sutherland GD (2000) Diversity of forest upland arachnid communities in Manitoba taiga (Araneae, Opiliones). Canadian Field-Naturalist 114 : 636–651

Akaike H (1973) Information theory as an extension of the maximum likelihood principle. In: Petrov BN, Csaki F (eds) 2nd International Symposium Information Theory. Akademia iKiado, Budapest, Hungary

Alday JG, Marrs RH, Martínez-Ruiz C (2012) Soil and vegetation development during early succession on restored coal wastes: a six-year permanent plot study. Plant and Soil 353 : 305–320

Allen RB, Lee WG (Eds.) (2006) Biological Invasions in New Zealand. Springer, Berlin, Germany

Allen RB, Partridge TR, Lee WG, Efford M (1992) Ecology of *Kunzea ericoides* (A. Rich.) J. Thompson (kanuka) in east Otago, New Zealand. New Zealand Journal of Botany 30 : 135–149

An S-S, Cheng Y, Huang Y-M, Liu D (2013) Effects of revegetation on soil microbial biomass, enzyme activities, and nutrient cycling on the Loess Plateau in China. Restoration Ecology 21 : 600–607

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecology 26 : 32–46

Anderson MJ, Walsh DCI (2013) PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? Ecological Monographs 83 : 557–574

Andreasen JK, O'Neill RV, Noss R, Slosser NC (2001) Considerations for the development of a terrestrial index of ecological integrity. Ecological Indicators 1 : 21–35

Angeler DG, Allen CR (2016) Quantifying resilience. Journal of Applied Ecology 53 : 617–624

Angermeier PL, Karr JR (1994) Biological integrity versus biological diversity as policy directives. BioScience 44 : 690–697

Anglo Platinum (2009) BBOP pilot project case study. Potgietersrust Platinums Limited (PPRust). Business and Biodiversity Offset Programme (BBOP), Johannesburg, South Africa http://bbop.forest-trends.org/guidelines/ index. php

Areola O, Aweto AO, Gbadegesin AS (1982) Organic matter and soil fertility restoration in forest and savanna fallows in southwestern Nigeria. GeoJournal 6 : 183–192

Aronson J, Floret C, Le Floc'h E, Ovalle C, Pontanier R (1993a) Restoration and rehabilitation of degraded ecosystems in arid and semi-arid lands.II. Case studies in Southern Tunisia, Central Chile and northern Cameroon. Restoration Ecology 1 : 168–187

Aronson J, Floret C, Le Floc'h E, Ovalle C, Pontanier R (1993b) Restoration and rehabilitation of degraded ecosystems in arid and semi-arid lands .I. A view from the South. Restoration Ecology 1 : 8–17

Arunachalam A, Pandey HN (2003) Ecosystem restoration of Jhum fallows in northeast India: microbial C and N along altitudinal and successional gradients. Restoration Ecology 11 : 168–173

Audino LD, Louzada J, Comita L (2014) Dung beetles as indicators of tropical forest restoration success: is it possible to recover species and functional diversity? Biological Conservation 169 : 248–257

Ayres E, Steltzer H, Simmons BL, Simpson RT, Steinweg JM, Wallenstein MD, Mellor N, Parton WJ, Moore JC, Wall DH (2009) Home-field advantage accelerates leaf litter decomposition in forests. Soil Biology and Biochemistry 41 : 606–610

Bacaro G, Baragatti E, Chiarucci A (2009) Using taxonomic data to assess and monitor biodiversity: are the tribes still fighting? Journal of Environmental Monitoring 11 : 798–801

Bailey JD, Covington WW (2002) Evaluating ponderosa pine regeneration rates following ecological restoration treatments in northern Arizona, USA. Forest Ecology and Management 155 : 271–278

Ballantine K, Schneider R (2009) Fifty-five years of soil development in restored freshwater depressional wetlands. Ecological Applications 19 : 1467–1480

Banks Peninsula Conservation Trust (2010) International year of biodiversity. Landnotes 21 : 1–8

Bannister JR, Donoso PJ (2013) Forest typification to characterize the structure and composition of old-growth evergreen forests on Chiloe Island, North Patagonia (Chile). Forests 4 : 1087–1105

Barbault R (2011) 2010: A new beginning for biodiversity? Comptes Rendus Biologies 334 : 483–488

Bardgett RD, Wardle DA (2010) Aboveground-belowground linkages: biotic interactions, ecosystem processes, and global change. Oxford University Press, New York, USA

Barratt BIP, Derraik JGB, Rufaut CG, Dickinson KJM (2003) Morphospecies as a substitute for Coleoptera species identification, and the value of experience in improving accuracy. Journal of the Royal Society of New Zealand 33 : 583–590

Battaglia LL, Pritchett DW, Minchin PR (2008) Evaluating dispersal limitation in passive bottomland forest restoration. Restoration Ecology 16 : 417–424

Bauhus J, Puettmann K, Messier C (2009) Silviculture for old-growth attributes. Forest Ecology and Management 258 : 525–537

Baylis GTS (1980) Mycorrhizas and the spread of beech. New Zealand Journal Of Ecology 3 : 151–153

BBOP (2009a) Biodiversity offset design handbook: appendices. Business and Biodiversity Offsets Programme (BBOP), Washington D.C.,USA http://bbop.forest-trends.org/guidelines/index.php

BBOP (2009b) Biodiversity offset design handbook. Business and Biodiversity Offsets Programme (BBOP), Washington D.C. http://bbop.forest-trends.org/guidelines/index.php

BBOP (2009c) Glossary. Business and Biodiversity Offsets Programme (BBOP), Washington D.C. http://bbop.forest-trends.org/guidelines/index.php

BBOP (2011) Resource paper: no net loss and loss-gain calculations in biodiversity offsets. Business and Biodiversity Offsets Programme (BBOP), Washington D.C., USA www.bbopconsultation.org/resourcepapers

BBOP (2012) Executive summary of BBOP standard, technical handbooks and resource papers. Business and Biodiversity Offsets Programme (BBOP), Washington D.C. http://bbop.forest-trends.org/guidelines/Handbook_ Summary.pdf

BBOP (2013) To no net loss and beyond: an overview of the business and biodiversity offsets programme (BBOP). Business and Biodiversity Offsets Programme (BBOP), Washington D.C. www.forest-trends.org/biodiversity offsetprogram/guidelines/Overview_II.pdf

Bedward M, Ellis M V., Simpson CC (2009) Simple modelling to assess if offsets schemes can prevent biodiversity loss, using examples from Australian woodlands. Biological Conservation 142 : 2732–2742

Benabou S (2014) Making up for lost nature? A critical review of the international development of voluntary biodiversity offsets. Environment and Society: Advances in Research 5 : 103–123

Bender DJ, Tischendorf L, Fahrig L (2003) Using patch isolation metrics to predict animal movement in binary landscapes. Landscape Ecology 18 : 17–39

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society. Series B (Methodological) 57 : 289–300

Berner PO, Dickson S, Andrianarimisa A (2009) BBOP pilot project case study. The Ambatovy project. Business and Biodiversity Offset Programme (BBOP) http://bbop.forest-trends.org/guidelines/index.php

Bhat A, Magurran AE (2006) Taxonomic distinctness in a linear system: a test using a tropical freshwater fish assemblage. Ecography 29 : 104–110

Bílek L, Vacek S, Vacek Z, Remeš J, Král J, Bulušek D, Gallo J (2016) How close to nature is close-to-nature pine silviculture? Journal of Forest Science 62 : 24–34

Billings WD (1938) The structure and development of old field shortleaf pine stands and certain associated physical properties of the soil. Ecological Monographs 8 : 437–500

Block WM, Franklin AB, Ward JP, Ganey JL, White GC (2001) Design and implementation of monitoring studies to evaluate the success of ecological restoration on wildlife. Restoration Ecology 9 : 293–303

Bocock KL, Gilbert OJW (1957) The disappearance of leaf litter under different woodland conditions. Plant and Soil 9 : 179–185

Boerner REJ, Coates AT, Yaussy DA, Waldrop TA (2008) Assessing ecosystem restoration alternatives in eastern deciduous forests: the view from belowground. Restoration Ecology 16 : 425–434

Bongers F, Poorter L, Hawthorne WD, Sheil D (2009) The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. Ecology Letters 12 : 798–805

Borders BD, Pushnik JC, Wood DM (2006) Comparison of leaf litter decomposition rates in restored and mature riparian forests on the Sacramento River, California. Restoration Ecology 14 : 308–315

Botta-Dukát Z (2005) Rao's quadratic entropy as a measure of functional diversity. Journal of Vegetation Science 16 : 533–540

Brady CJ, Noske R a. (2010) Succession in bird and plant communities over a 24-year chronosequence of mine rehabilitation in the Australian monsoon tropics. Restoration Ecology 18 : 855–864

Brancalion PHS, Holl KD (2016) Functional composition trajectory: a resolution to the debate between Suganuma, Durigan, and Reid. Restoration Ecology 24 : 1–3

Bray JR (1989) The use of historical vegetation dynamics in interpreting prehistorical vegetation change. Journal of the Royal Society of New Zealand 19 : 151–160

Bray JR, Burke WD, Struik GJ (1999) Propagule dispersion and forest regeneration in *Leptospermum scoparium* (manuka) - *L. ericoides* (kanuka) forests following fire in Golden Bay, New Zealand. New Zealand Natural Sciences 24 : 35–52

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of Southern Wisconsin. Ecological Monographs 27 : 325–349

Brennan KEC, Ashby L, Majer JD, Moir ML, Koch JM (2006) Simplifying assessment of forest management practices for invertebrates: how effective are higher taxon and habitat surrogates for spiders following prescribed burning? Forest Ecology and Management 231 : 138–154

Briones MJI (2014) Soil fauna and soil functions: a jigsaw puzzle. Frontiers in

Environmental Science 2 : 1–22

Brokaw NVL, Lent RA (1999) Vertical Structure. Pages 373–399 In: Hunter Jr ML (ed) Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge,United Kingdom

Brudvig LA (2011) The restoration of biodiversity: where has research been and where does it need to go? American Journal of Botany 98 : 549–58

Buckland ST, Magurran AE, Green RE, Fewster RM (2005) Monitoring change in biodiversity through composite indices. Philosophical Transactions of the Royal Society B 360 : 243–54

Bull JW, Suttle KB, Gordon A, Singh NJ, Milner-Gulland EJ (2013) Biodiversity offsets in theory and practice. Oryx 47 : 369–380

Bultman TL, Uetz GW (1982) Abundance and community structure of forest floor spider communities following litter manipulation. Oecologia 55 : 34–41

Burgin S (2008) BioBanking: an environmental scientist's view of the role of biodiversity banking offsets in conservation. Biodiversity and Conservation 17 : 807–816

Burrows CJ (1973) The ecological niches of *Leptospermum scoparium* and *L. ericoides* (Angiospermae: Myrtaceae). MAURI ORA 1 : 5–12

Burrows CJ (1994a) Fruit, seeds, birds and the forests of Banks Peninsula. New Zealand Natural Sciences 21 : 87–108

Burrows CJ (1994b) Fruit types and seed dispersal modes of woody plants in Ahuriri Summit Bush, Port Hills, western Banks Peninsula, Canterbury, New Zealand. New Zealand Journal of Botany 32 : 169–181

Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, … Watson R (2010) Global biodiversity: indicators of recent declines. Science 328 : 1164–1168

Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48 : 1079–1087

Callaham MA, Rhoades CC, Heneghan L (2008) A striking profile: soil ecological knowledge in restoration management and science. Restoration Ecology 16 : 604–607

Carignan V, Villard M-A (2002) Selecting indicator species to monitor ecological integrity: a review. Environmental Monitoring and Assessment 78 : 45–61

Caro T (2010) Environmental indicator species. Pages 159–186 In: Conservation by proxy: indicator, umbrella, keystone, flagship, and other surrogate species. Island Press, Washington D.C.

Castro-Luna AA, Sosa VJ, Castillo-Campos G (2007) Bat diversity and abundance associated with the degree of secondary succession in a tropical forest mosaic in south-eastern Mexico. Animal Conservation 10 : 219–228

Catford JA, Daehler CC, Murphy HT, Sheppard AW, Hardesty BD, Westcott DA,

Rejmánek M, Bellingham PJ, Pergl J, Horvitz CC, Hulme PE (2012) The intermediate disturbance hypothesis and plant invasions: implications for species richness and management. Perspectives in Plant Ecology, Evolution and Systematics 14 : 231–241

Chao A, Chazdon RL, Colwell RK, Shen TJ (2006) Abundance-based similarity indices and their estimation when there are unseen species in samples. Biometrics 62 : 361–371

Chao A, Chiu CH, Jost L (2016) Statistical challenges of evaluating diversity patterns across environmental gradients in mega-diverse communities. Journal of Vegetation Science 27 : 437–438

Chao A, Gotelli NJ, Hsieh TC, Sander EL, Colwell RK, Ellison AM (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs 84 : 45–67

Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93 : 2533–47

Chao A, Lee S-M (1992) Estimating the number of classes via sample coverage. Journal of the American Statistical Association 87 : 210–217

Chazdon RL, Letcher SG, van Breugel M, Martínez-Ramos M, Bongers F, Finegan B (2007) Rates of change in tree communities of secondary neotropical forests following major disturbances. Philosophical Transactions of the Royal Society B 362 : 273–289

Chiarucci A, Bacaro G, Scheiner SM (2011) Old and new challenges in using species diversity for assessing biodiversity. Philosophical Transactions of the Royal Society B 366 : 2426–2437

Chillo V, Anand M, Ojeda RA (2011) Assessing the use of functional diversity as a measure of ecological resilience in arid rangelands. Ecosystems 14 : 1168–1177

Chu-Chou M, Grace LJ (1987) Mycorrhizal fungi of *Pinus radiata* in New Zealand. New Zealand Journal of Forestry Science 17 : 76–82

City of Bainbridge Island (2009) Pilot project case study. Bainbridge Island. Business and Biodiversity Offsets Programme (BBOP), Washington State, USA http://bbop.forest-trends.org/guidelines/index.php

Clarke KR, Somerfield PJ, Chapman MG (2006) On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. Journal of Experimental Marine Biology and Ecology 330 : 55–80

Clarke KR, Warwick RM (1998) A taxonomic distinctness index and its statistical properties. Journal of Applied Ecology 35 : 523–531

Clarke KR, Warwick RM (2001) A further biodiversity index applicable to species lists: variation in taxonomic distinctness. Marine Ecology Progress Series

216 : 265–278

Clewell AF, Aronson J (2013) Disturbance and impairment. Pages 33–70 In: Ecological restoration: principles, values, and structure of an emerging science. Island Press, Washington D.C.

Cole RJ, Holl KD, Zahawi RA, Wickey P, Townsend AR (2016) Leaf litter arthropod responses to tropical forest restoration. Ecology and Evolution 6 : 5158–5168

Coleman DC, Crossley DAJ, Hendrix PF (2004) Fundamentals of Soil Ecology. Elsevier Academic Press, San Diego, USA

Coomes DA, Allen RB (2016) Mortality and tree-size distributions in natural mixed-age forests. Journal of Ecology 62 : 182–190

Couteaux MM, Bottner P, Berg B (1995) Litter decomposition climate and litter quality. Trends in Ecology and Evolution 10 : 63–66

Cowles HC (1899) The ecological relations of the vegetation on the sand dunes of Lake Michigan. Botanical Gazette 27 : 95–117, 167– 202, 281–308, 361–391

Cramer VA, Hobbs RJ, Standish RJ (2008) What's new about old fields? Land abandonment and ecosystem assembly. Trends in Ecology and Evolution 23 : 104–12

Cristescu RH, Rhodes J, Frére C, Banks PB (2013) Is restoring flora the same as restoring fauna? Lessons learned from koalas and mining rehabilitation. Journal of Applied Ecology 50 : 423–431

Crooks KR (2002) Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16 : 488–502

Cumming GS (2011) Spatial resilience: integrating landscape ecology, resilience, and sustainability. Landscape Ecology 26 : 899–909

Curran M, Hellweg S, Beck J (2014) Is there any empirical support for biodiversity offset policy? Ecological Applications 24 : 617–632

De Cáceres M, Font X, Oliva F (2010) The management of vegetation classifications with fuzzy clustering. Journal of Vegetation Science 21 : 1138–1151

De Leo GA, Levin S (1997) The multifaceted aspects of ecosystem integrity. Conservation Ecology [Online]. (Available from http://www.consecol.org/vol1/iss1/art3/) 1(1):3

Delang CO, Li WM (2013) Forest Structure. Pages 9–38 In: Ecological succession on fallowed shifting cultivation fields. Springer, Dordrecht, Netherlands

Dent DH, Dewalt SJ, Denslow JS (2013) Secondary forests of central Panama increase in similarity to old-growth forest over time in shade tolerance but not species composition. Journal of Vegetation Science 24 : 530–542

Derhé MA, Murphy H, Monteith G, Menéndez R (2016) Measuring the success of reforestation for restoring biodiversity and ecosystem functioning. Journal of Applied Ecology 53 : 1714–1724

Derraik JGB, Closs GP, Dickinson KJM, Sirvid P, Barratt BIP, Patrick BH (2002) Arthropod morphospecies versus taxonomic species: a case study with Araneae, Coleoptera, and Lepidoptera. Conservation Biology 16 : 1015–1023

Desrochers RE, Anand M (2004) From traditional diversity indices to taxonomic diversity indices. International Journal of Ecology and Environmental Sciences 30 : 85–92

Diamond JM (1989) Overview of recent extinctions. Pages 37–41 In: Western D, Pearl MC (eds) In conservation for the twenty-first century. Oxford University Press, USA

Dickie IA, Davis M, Carswell FE (2012) Quantification of mycorrhizal limitation in beech spread. New Zealand Journal of Ecology 36 : 210–215

Dickinson Y, Pelz K, Giles E, Howie J (2016) Have we been successful? Monitoring horizontal forest complexity for forest restoration projects. Restoration Ecology 24 : 8–17

Didham RK, Barker GM, Costall JA, Denmead LH, Floyd CG, Watts CH (2009) The interactive effects of livestock exclusion and mammalian pest control on the restoration of invertebrate communities in small forest remnants. New Zealand Journal of Zoology 36 : 135–163

DOC (2014) Guidance on good practice biodiversity offsetting in New Zealand. Department of Conservation (DOC), Wellington, New Zealand, p. 44

Dodson EK, Burton JI, Puettmann KJ (2014) Multiscale controls on natural regeneration dynamics after partial overstory removal in Douglas-fir forests in western Oregon, USA. Forest Science 60 : 1–10

Dornelas M, Soykan CU, Ugland KI (2011) Biodiversity and disturbance. Pages 237–251 In: Magurran AE, McGill B (eds) Biological diversity: frontiers in measurement and assessment. Oxford University Press, New York

Drever CR, Peterson G, Messier C, Bergeron Y, Flannigan M (2006) Can forest management based on natural disturbances maintain ecological resilience? Canadian Journal of Forest Research 36 : 2285–2299

Du F, Shao HB, Shan L, Liang ZS, Shao MA (2007) Secondary succession and its effects on soil moisture and nutrition in abandoned old-fields of hilly region of Loess Plateau, China. Colloids and Surfaces B: Biointerfaces 58 : 278–285

Duduman G (2011) A forest management planning tool to create highly diverse uneven-aged stands. Forestry 84 : 301–314

Durigan G, Suganuma MS (2015) Why species composition is not a good indicator to assess restoration success? Counter-response to Reid (2015). Restoration Ecology 23 : 521–523

Egunjobi JK (1971a) Ecosystem processes in a stand of *Ulex europaeus L.*: I. dry matter production, litter fall and efficiency of solar energy utilization. The Journal of Ecology 59 : 31–38

Egunjobi JK (1971b) Ecosystem processes in a stand of *Ulex europaeus L.*: II. the cycling of chemical elements in the ecosystem. The Journal of Ecology 59 :

669–678

Ehrenfeld JG, Toth LA (1997) Restoration ecology and the ecosystem perspective. Restoration Ecology 5 : 307–317

Eijsackers H, Zehnder AJB (1990) Litter decomposition: a Russian matriochka doll. Biogeochemistry 11 : 153–174

Elmqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, Norberg J (2003) Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment 1 : 488–494

Engst K, Baasch A, Erfmeier A, Jandt U, May K, Schmiede R, Bruelheide H (2016) Functional community ecology meets restoration ecology: Assessing the restoration success of alluvial floodplain meadows with functional traits. Journal of Applied Ecology 53 : 751–764

Esler AE (1978) Botanical features of Tiritiri Island, Hauraki Gulf ,New Zealand. New Zealand Journal of Botany 16 : 207–226

ESRI (2011) ArcGIS Desktop: Release 10. CA: Environmental Systems Research Institute, Redlands, USA

Eviner VT, Hawkes CV (2008) Embracing variability in the application of plant-soil interactions to the restoration of communities and ecosystems. Restoration Ecology 16 : 713–729

Fahrig L, Merriam G (1994) Conservation of fragmented populations. Conservation Biology 8 : 50–59

Failing L, Gregory R (2003) Ten common mistakes in designing biodiversity indicators for forest policy. Journal of Environmental Management 68 : 121–132

Faith DP, Minchin PR, Belbin L (1987) Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69 : 57–68

Fang W, Peng S (1997) Development of species diversity in the restoration process of establishing a tropical man made forest ecosystem in China. Forestry Ecology and Management 99 : 185–196

Feest A (2006) Establishing baseline indices for the quality of the biodiversity of restored habitats using a standardized sampling process. Restoration Ecology 14 : 112–122

Feldpausch TR, Rondon MA, Fernandes ECM, Riha SJ, Wandelli E (2004) Carbon and nutrient accumulation in secondary forests regenerating on pastures in central Amazonia. Ecological Applications 14 : S164–S176

Ferlian O, Scheu S (2014) Shifts in trophic interactions with forest type in soil generalist predators as indicated by complementary analyses of fatty acids and stable isotopes. Oikos 123 : 1182–1191

Ferris R, Humphrey JW (1999) A review of potential biodiversity indicators for application in British forests. Forestry 72 : 313–328

Fiala ACS, Garman SL, Gray AN (2006) Comparison of five canopy cover

estimation techniques in the western Oregon Cascades. Forest Ecology and Management 232 : 188–197

Fierke MK, Kauffman JB (2005) Structural dynamics of riparian forests along a black cottonwood successional gradient. Forest Ecology and Management 215 : 149–162

Flynn DFB, Mirotchnick N, Jain M, Palmer MI, Naeem S (2011) Functional and phylogenetic diversity as predictors of biodiversity-ecosystem-function relationships. Ecology 92 : 1573–81

Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS (2004) Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology, Evolution, and Systematics 35 : 557–581

Forman RTT, Godron M (1981) Patches and structural components for a landscape ecology. BioScience 31 : 733–740

Franken RJ, Hik DS (2004) Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas *Ochotona collaris*. Journal of Animal Ecology 73 : 889–896

Franklin JF, Cromack K, Denison W, McKee A, Maser C, Sedell J, Swanson F, Juday G (1981) Ecologcial characteristics of old-growth Douglas-fir forests. General technical report PNW-118. USDA Forest Service, Portland, USA

Franklin JF, Lindenmayer DB, Thornburgh DA, Pelt R Van, Chen J, Spies TA, Carey AB, Shaw DC, Berg DR, Harmon ME, Keeton WS, Bible K (2002) Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155 : 399–423

Fuhlendorf SD, Zhang H, Tunnell TR, Engle DM, Cross AF (2002) Effects of grazing on restoration of southern mixed prairie soils. Restoration Ecology 10 : 401–407

Funk JL, Cleland EE, Suding KN, Zavaleta ES (2008) Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology and Evolution 23 : 695–703

Gardner TA, Von Hase A, Brownlie S, Ekstrom JMM, Pilgrim JD, Savy CE, Stephens RTT, Treweek J, Ussher GT, Ward G, Ten Kate K (2013) Biodiversity offsets and the challenge of achieving no net loss. Conservation Biology 27 : 1254–1264

Gerlach J, Samways M, Pryke J (2013) Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. Journal of Insect Conservation 17 : 831–850

Gerschefske KD, Hetrick BAD, Wilson GWT (1988) Relationship of soil fertility to suppression of the growth response of mycorrhizal big bluestem in non-sterile soil. New Phytologist 109 : 473–481

Gibbons P, Evans MC, Maron M, Gordon A, Le Roux D, von Hase A,

Lindenmayer DB, Possingham HP (2016) A loss-gain calculator for biodiversity offsets and the circumstances in which no net loss is feasible. Conservation Letters 9 : 252–259

Gibbons P, Freudenberger D (2006) An overview of methods used to assess vegetation condition at the scale of the site. Ecological Management & Restoration 7 : S10–S17

Gil-Sotres F, Trasar-Cepeda C, Leirós MC, Seoane S (2005) Different approaches to evaluating soil quality using biochemical properties. Soil Biology & Biochemistry 37 : 877–887

Gini C (1912) Variabilità e mutabilità.Bologna, Italy

Gomes ACS, Luizão FJ (2012) Leaf and soil nutrients in a chronosequence of second-growth forest in central Amazonia: implications for restoration of abandoned lands. Restoration Ecology 20 : 339–345

Gonçalves B, Marques A, Soares AMVDM, Pereira HM (2015) Biodiversity offsets: from current challenges to harmonized metrics. Current Opinion in Environmental Sustainability 14 : 61–67

Gonsamo A, D'Odorico P, Pellikka P (2013) Measuring fractional forest canopy element cover and openness - definitions and methodologies revisited. Oikos 122 : 1283–1291

Goosem M, Paz C, Fensham R, Preece N, Goosem S, Laurance SGW (2016) Forest age and isolation affect the rate of recovery of plant species diversity and community composition in secondary rain forests in tropical Australia. Journal of Vegetation Science 27 : 504–514

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4 : 379–391

Gotelli NJ, Colwell RK (2011) Estimating species richness. Pages 39–54 In: Magurran AE, McGill BJ (eds) Biological diversity: frontiers in measurement and assessment. Oxford University Press, New York, USA

Gould SF (2012) Comparison of post-mining rehabilitation with reference ecosystems in monsoonal eucalypt woodlands, Northern Australia. Restoration Ecology 20 : 250–259

Gould SF, Mackey BG (2015) Site vegetation characteristics are more important than landscape context in determining bird assemblages in revegetation. Restoration Ecology (in press)

Grant CD, Ward SC, Morley SC (2007) Return of ecosystem function to restored bauxite mines in western Australia. Restoration Ecology 15 : S94–S103

Grantham HS, Pressey RL, Wells JA, Beattie AJ (2010) Effectiveness of biodiversity surrogates for conservation planning: different measures of effectiveness generate a kaleidoscope of variation. PloS ONE 5 : e11430

Grelle CEV (2003) Forest structure and vertical stratification of small mammals in a secondary Atlantic Forest, southeastern Brazil. Studies on Neotropical

Fauna and Environment 38 : 81–85

Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Reviews 52 : 107–145

Guariguata M (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. Forest Ecology and Management 148 : 185–206

Hallett LM, Diver S, Eitzel M V, Olson JJ, Ramage BS, Sardinas H, Statman-Weil Z, Suding KN (2013) Do we practice what we preach? Goal setting for ecological restoration. Restoration Ecology 21 : 312–319

Hanford JK, Crowther MS, Hochuli DF (2017) Effectiveness of vegetation-based biodiversity offset metrics as surrogates for ants. Conservation Biology 31 : 161–171

Hansen RA (2000) Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. Ecology 81 : 1120–1132

Hanson JJ, Lorimer CG, Halpin CR (2011) Predicting long-term sapling dynamics and canopy recruitment in northern hardwood forests. Canadian Journal of Forest Research 41 : 903–919

Harris JA (2003) Measurements of the soil microbial community for estimating the success of restoration. European Journal of Soil Science 54 : 801–808

Harris RJ, Toft RJ, Dugdale JS, Williams PA, Rees JS (2004) Insect assemblages in a native (kanuka-*Kunzea ericoides*) and an invasive (gorse-*Ulex europaeus*) shrubland. New Zealand Journal of Ecology 28 : 35–47

Harvey M, Pilgrim S (2011) The new competition for land: food, energy, and climate change. Food Policy 36 : S40–S51

Haselwandter K (1997) Soil micro-organism, mycorrhiza, and restoration ecology. Pages 65–80 In: Urbanska KM, Webb NR, Edwards PJ (eds) Restoration ecology and sustainable development. Cambridge University Press, Cambridge, United Kingdom

Hedberg P, Saetre P, Sundberg S, Rydin H, Kotowski W (2013) A functional trait approach to fen restoration analysis. Applied Vegetation Science 16 : 658–666

Heink U, Kowarik I (2010) What criteria should be used to select biodiversity indicators? Biodiversity and Conservation 19 : 3769–3797

Heino J, Mykrä H, Hämäläinen H, Aroviita J, Muotka T (2007) Responses of taxonomic distinctness and species diversity indices to anthropogenic impacts and natural environmental gradients in stream macroinvertebrates. Freshwater Biology 52 : 1846–1861

Heip CHR, Herman PMJ, Soetaert K (1998) Indices of diversity and evenness *. Oceanis 24 : 61–87

Heiri C, Wolf A, Rohrer L, Brang P, Bugmann H (2012) Successional pathways in Swiss mountain forest reserves. European Journal of Forest Research 131 : 503–518

Helmus MR, Keller W, Paterson MJ, Yan ND, Cannon CH, Rusak JA (2010) Communities contain closely related species during ecosystem disturbance. Ecology Letters 13 : 162–174

Hervé M (2016) RVAideMemoire: diverse basic statistical and graphical functions. (available from https://cran.r-project.org/package=RVAideMemoire)

Hessenmoeller D, Elsenhans AS, Schulze ED (2013) Sampling forest tree regeneration with a transect approach. Annals of Forest Research 56 : 3–14

Hilderbrand RH, Watts AC, Randle AM (2005) The myths of restoration ecology. Ecology and Society 10 : 1–19

Hill MO (1973) Diversity and evenness: a unifying notation and its consequences. Ecology 54 : 427–432

Hobbs RJ, Arico S, Aronson J, Baron JS, Cramer VA, Epstein PR, Ewel JJ, Klink CA, Lugo AE, Norton D, Ojima D, Richardson DM (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15 : 1–7

Hobbs RJ, Higgs E, Harris JA (2009) Novel ecosystems: implications for conservation and restoration. Trends in Ecology & Evolution 24 : 599–605

Hobbs RJ, Higgs ES, Hall CM (2013) What do we know about, and what do we do about, novel ecosystems? Pages 353–360 In: Novel ecosystems: intervening in the new ecological world order. Wiley-Blackwell, West Sussex, UK

Hodgson D, McDonald JL, Hosken DJ (2015) What do you mean, "resilient"? Trends in Ecology and Evolution 30 : 503–506

Holl KD, Loik ME, Lin EH V, Samuels IA (2000) Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. Restoration Ecology 8 : 339–349

Holm S (1979) A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6 : 65–70

Honnay O, Jacquemyn H, Bossuyt B, Hermy M (2005) Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. New Phytologist 166 : 723–736

Hopp PW, Ottermanns R, Caron E, Meyer S, Roß-Nickoll M (2010) Recovery of litter inhabiting beetle assemblages during forest regeneration in the Atlantic forest of Southern Brazil. Insect Conservation and Diversity 3 : 103–113

Hsieh TC, Ma KH, Chao A (2016) iNEXT: interpolation and extrapolation for species diversity. R package version 2.0.8. (available from url: http://chao.stat.nthu.edu.tw/blog/software-download)

Hunter Jr. ML (1999) Biological diversity. Pages 3–21 In: Hunter Jr ML (ed) Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge,United Kingdom

Hurd LE, Fagan WF (1992) Cursorial spiders and succession: age or habitat

structure? Oecologia 92 : 215–221

Hurlbert SH (1971) The nonconcept of species diversity: a critique and alternative parameters. Ecology 52 : 577–586

Hurst JM, Allen RB (2007) The Recce method for describing New Zealand vegetation: field protocols. Landcare Research, Lincoln, New Zealand https://nvs.landcareresearch.co.nz/Content/Recce_FieldProtocols.pdf

ICMM, IUCN (2012) Independent report on biodiversity offsets. The Biodiversity Consultancy www.icmm.com/biodiversity-offsets

Ingle NR (2003) Seed dispersal by wind, birds, and bats between Philippine montane rainforest and successional vegetation. Oecologia 134 : 251–261

Jaccard P (1912) The distribution of the flora in the alpine zone. New Phytologist 11 : 37–50

Jansen A (1997) Terrestrial invertebrate community structure as an indicator of the success of a tropical rainforest restoration project. Restoration Ecology 5 : 115–124

Janzen DH (1990) An abandoned field is not a tree fall gap. Vida Silvestre Neotropical 2 : 64–67

Jasper DA (2007) Beneficial soil microorganisms of the jarrah forest and their recovery in bauxite mine restoration in southwestern Australia. Restoration Ecology 15 : S74–S84

Jennings SB, Brown ND, Sheil D (1999) Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. Forestry 72 : 59–73

Johns PM (1962) Introduction to the endemic and introduced millipedes of New Zealand. New Zealand Entomologist 3 : 38–46

Johns PM (2015a) Key to Myriapoda (Unpublished manuscript). Canterbury Museum, Christchurch, New Zealand

Johns PM (2015b) New Zealand Chilopoda (Unpublished manuscript). Canterbury Museum, Christchurch, New Zealand

Johnson EA, Miyanishi K (2008) Testing the assumptions of chronosequences in succession. Ecology Letters 11 : 419–431

Jones HP, Schmitz OJ (2009) Rapid recovery of damaged ecosystems. PloS ONE 4 : e5653

Jost L (2006) Entropy and diversity. Oikos 113 : 363–375

Jost L (2010) The relation between evenness and diversity. Diversity 2 : 207–232

Jost L, Chao A, Chazdon RL (2011) Compositional similarity and β (beta) diversity. Pages 66–84 In: Magurran AE, Mcgill BJ (eds) Biological diversity: frontiers in measurement and assessment. Oxford University Press, Oxford, USA

Kaennel M (1998) Biodiversity: a diversity in definition. In: Bachmann P, Köhl

M, Päivinen R (eds) Assessment of biodiversity for improved forest planning. Kluwer Academic Publishers, Dordrecht, Netherlands

Kalinkat G, Brose U, Rall BC (2013) Habitat structure alters top-down control in litter communities. Oecologia 172 : 877–887

Kanowski J, Catterall CP, Wardell-Johnson GW, Proctor H, Reis T (2003) Development of forest structure on cleared rainforest land in eastern Australia under different styles of reforestation. Forest Ecology and Management 183 : 265–280

Kardol P, Bezemer TM, Van Der Putten WH (2006) Temporal variation in plant-soil feedback controls succession. Ecology Letters 9 : 1080–1088

Kardol P, Bezemer TM, Van Der Wal A, Van Der Putten WH (2005) Successional trajectories of soil nematode and plant communities in a chronosequence of ex-arable lands. Biological Conservation 126 : 317–327

Kardol P, Wardle DA (2010) How understanding aboveground-belowground linkages can assist restoration ecology. Trends in Ecology & Evolution 25 : 670–679

Kiesecker JM, Copeland H, Pocewicz A, Nibbelink N, McKenney B, Dahlke J, Holloran M, Stroud D (2009) A framework for implementing biodiversity offsets: selecting sites and determining scale. BioScience 59 : 77–84

Kindt R, Coe R (2005) Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre (ICRAF), Nairobi, Kenya http://cran.r-project.org/package=BiodiversityR

Klimaszewski J, Watt JC (1997) Coleoptera: family-group review and keys to identification. Fauna of New Zealand No. 37 (C. T. Duval, Ed.). Manaaki Whenua Press, Lincoln, New Zealand

Koch JM, Hobbs RJ (2007) Synthesis: is Alcoa successfully restoring a jarrah forest ecosystem after bauxite mining in western Australia? Restoration Ecology 15 : S137–S144

Koivula M, Punttila P, Haila Y, Niemela J (1999) Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. Ecography 22 : 424–435

Kraft G (1884) Beiträge zur Lehre von Durchforstungen, Schlagstellungen und Lichtungshieben (Vol. 167). Klindworth's Verlag, Hannover, Germany

Kwok ABC, Eldridge DJ, Oliver I (2011) Do landscape health indices reflect arthropod biodiversity status in the eucalypt woodlands of eastern Australia? Austral Ecology 36 : 800–813

Lalibert E (2011) Land-use intensification in grazing systems: plant trait responses and feedbacks to ecosystem functioning and resilience. PhD thesis, University of Canterbury, New Zealand

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91 : 299–305

Laliberté E, Legendre P, Shipley B (2014) Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R package version 1.0-12.

Laliberté E, Wells JA, DeClerck F, Metcalfe DJ, Catterall CP, Queiroz C, Aubin I, Bonser SP, Ding Y, Fraterrigo JM, McNamara S, Morgan JW, Merlos DS, Vesk PA, Mayfield MM (2010) Land-use intensification reduces functional redundancy and response diversity in plant communities. Ecology Letters 13 : 76–86

Lamb EG, Bayne E, Holloway G, Schieck J, Boutin S, Herbers J, Haughland DL (2009) Indices for monitoring biodiversity change: are some more effective than others? Ecological Indicators 9 : 432–444

Langer ERL, Davis MR, Ross CW (1999) Rehabilitation of lowland indigenous forest after mining in Westland. Science for Conservation 117. Department of Conservation, Wellington, New Zealand http://www.crl.co.nz/downloads/geology/1999/Langer_et_al_1999_Rehab_of_lowland_forest_SFC.pdf?np=y

Laughlin DC (2014) Applying trait-based models to achieve functional targets for theory-driven ecological restoration. Ecology Letters 17 : 771–784

Lavelle P (1997) Faunal activities and soil processes: adaptive strategies that determine ecosystem function Advances in Ecological Research (Vol. 27)

Leadley P, Pereira HM, Alkemade R, Fernandez-Manjarrés, J F Proença V, Scharlemann JPW, Walpole MJ (2010) Biodiversity scenarios: projections of 21st century change in biodiversity and associated ecosystem services. Technical Series (Vol. 50). Secretariat of the Convention on Biological Diversity, Montreal, Canada

Leathwick JR (1998) Are New Zealand's *Nothofagus* species in equilibrium with their environment? Journal of Vegetation Science 9 : 719–732

Leathwick JR, Overton JM, McLeod M (2003) An environmental domain classification of New Zealand and its use as a tool. Conservation Biology 17 : 1612–1623

Lebrija-Trejos E, Meave JA, Poorter L, Pérez-García EA, Bongers F (2010) Pathways, mechanisms and predictability of vegetation change during tropical dry forest succession. Perspectives in Plant Ecology, Evolution and Systematics 12 : 267–275

Lee WG, Allen RB, Johnson PN (1986) Succession and dynamics of gorse (*Ulex europaeus L .*) communities in the dunedin ecological district South Island , New Zealand. New Zealand Journal of Botany 24 : 279–292

Lee WG, McGlone M, Wright E (2005) Biodiversity inventory and monitoring: a review of national and international systems and a proposed framework for future biodiversity monitoring by the Department of Conservation. Contract report LC0405/122. Landcare Research, Wellington, New Zealand http://www.landcareresearch.co.nz/publications/researchpubs/biodiv_inventory_system_review_framework.pdf

Legendre P, Legendre L (1998) Numerical ecology (2nd Englis.). Elsevier, Amsterdam, The Netherlands

Leighton Reid J (2015) Indicators of success should be sensitive to compositional failures: reply to Suganuma and Durigan. Restoration Ecology 23 : 519–520

Leinster T, Cobbold CA (2012) Measuring diversity: the importance of species similarity. Ecology 93 : 477–489

Lexerød NL, Eid T (2006) An evaluation of different diameter diversity indices based on criteria related to forest management planning. Forest Ecology and Management 222 : 17–28

Liebsch D, Marques M, Goldenberg R (2008) How long does the Atlantic Rain Forest take to recover after a disturbance? Changes in species composition and ecological features during secondary succession. Biological Conservation 141 : 1717–1725

Lohbeck M, Poorter L, Paz H, Pla L, van Breugel M, Martínez-Ramos M, Bongers F (2012) Functional diversity changes during tropical forest succession. Perspectives in Plant Ecology, Evolution and Systematics 14 : 89–96

Loranger G, Bandyopadhyaya L, Razaka B, Ponge J-F (2001) Does soil acidity explain altitudinal sequences in collembolan communities? Soil Biology and Biochemistry 33 : 381–393

Madsen B, Carroll N, Moore Brands K (2010) State of biodiversity markets report: offset and compensation programs worldwide. http://www.ecosystemmarketplace.

Magurran AE (2004) Measuring biological diversity. Blackwell Science Ltd., Oxford, UK

Magurran AE (2005) Biological diversity. Current Biology 15 : R116–R118

Majer JD, Brennan KEC, Moir ML (2007) Invertebrates and the restoration of a forest ecosystem: 30 years of research following bauxite mining in western Australia. Restoration Ecology 15 : S104–S115

Mallis RE, Hurd LE (2005) Diversity among ground-dwelling spider assemblages: habitat generalists and specialists. Journal of Arachnology 33 : 101–109

Marchetti MP, Garr M, Smith ANH (2010) Evaluating wetland restoration success using aquatic macroinvertebrate assemblages in the Sacramento Valley, California. Restoration Ecology 18 : 457–466

Maron M, Hobbs RJ, Moilanen A, Matthews JW, Christie K, Gardner TA, Keith DA, Lindenmayer DB, McAlpine CA (2012) Faustian bargains? Restoration realities in the context of biodiversity offset policies. Biological Conservation 155 : 141–148

Maron M, Ives CD, Kujala H, Bull JW, Maseyk FJF, Bekessy S, Gordon A, Watson JEM, Lentini PE, Gibbons P, Possingham HP, Hobbs RJ, Keith DA, Wintle BA, Evans MC (2016) Taming a wicked problem: resolving

controversies in biodiversity offsetting. BioScience 66 : 489–498

Maseyk F, Barea L, Stephens R, Possingham H, Dutson G, Maron M (2016) A disaggregated biodiversity offset accounting model to improve estimation of ecological equivalency and no net loss. Biological Conservation 204 : 322–332

Mason NWH, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional and functional evenness divergence: the primary of functional components diversity. Oikos 111 : 112–118

Mason NWH, Peltzer DA, Richardson SJ, Bellingham PJ, Allen RB (2010) Stand development moderates effects of ungulate exclusion on foliar traits in the forests of New Zealand. Journal of Ecology 98 : 1422–1433

Matthews TJ, Whittaker RJ (2015) On the species abundance distribution in applied ecology and biodiversity management. Journal of Applied Ecology 52 : 443–454

Maurer BA, McGill BJ (2011) Measurement of species diversity. Pages 55–65 In: Magurran AE, McGill BJ (eds) Biological diversity: frontiers in measurement and assessment. Oxford University Press, New York , USA

Mawson PR (1986) A comparative study of arachnid communities in rehabilitated bauxite mines. Western Australian Institute of Technology, School of Biology Bulletin 14 : 1–46

May RM (2002) The future of biological diversity in a crowded world. Current Science 82 : 1325–1331

Mayor SJ, Boutin S, He F, Cahill JF (2015) Limited impacts of extensive human land use on dominance, specialization, and biotic homogenization in boreal plant communities. BMC Ecology 15 : 1–11

Maza-Villalobos S, Balvanera P, Martínez-Ramos M (2011) Early regeneration of tropical dry forest from abandoned pastures: contrasting chronosequence and dynamic approaches. Biotropica 43 : 666–675

McCracken IJ (1993) Natural succession as a management strategy for gorse and broom covered land: minimum interference management. Canterbury Contract report for Canterbury Regional Council, Christchurch, New Zealand

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach. Oregon, USA

McElhinny C, Gibbons P, Brack C, Bauhus J (2005) Forest and woodland stand structural complexity: its definition and measurement. Forest Ecology and Management 218 : 1–24

McGuinness KA (1984) Species-area curves. Biological Reviews 59 : 423–440

McShane TO, Hirsch PD, Trung TC, Songorwa AN, Kinzig A, Monteferri B, Mutekanga D, Thang H Van, Dammert JL, Pulgar-Vidal M, Welch-Devine M, Brosius JP, Coppolillo P, O'Connor S (2011) Hard choices: making trade-offs between biodiversity conservation and human well-being. Biological Conservation 144 : 966–972

Meloni F, Varanda EM (2015) Litter and soil arthropod colonization in reforested semi-deciduous seasonal Atlantic forests. Restoration Ecology 23 : 690–697

Merigot B, Bertrand JA, Mazouni N, Mante C, Durbec JP, Gaertner JC (2007) A multi-component analysis of species diversity of groundfish assemblages on the continental shelf of the Gulf of Lions (north-western Mediterranean Sea). Estuarine, Coastal and Shelf Science 73 : 123–136

Miller C, Wells A (2003) Cattle grazing and the regeneration of totara (*Podocarpus totara var. waihoensis*) on river terraces, south Westland, New Zealand. New Zealand Journal of Ecology 27 : 37–44

Miller RB (1968) Flow and cycles of macro- and micro-elements in a forest soil and its environment. In: Transactions of the 9th International Congress of Soil Science, Adelaide, Australia. Volume IV. International Society of Soil Science and Angus and Robertson, Sydney, Australia

Ministry for the Environment (2011) Proposed national policy statment on indigenous biodiversity: evaluation under section 32 of the Resource Management Act 1991. Ministry for the Environment, Wellington, New Zealand

Ministry for the Environment, Department of Conservation (2000) The New Zealand biodiversity strategy: our chance to turn the tide. Department of Conservation and the Ministry for the Environment, Wellington, New Zealand

Minor MA, Robertson AW (2006) Soil bugs - an illustrated guide to New Zealand soil invertebrates. (available from http://soilbugs.massey.ac.nz/).

Mitchell RA (2005) A comparison of three natural succession chronosequence case studies from the South Island, New Zealand to select predictable indices for evaluating restoration success. PhD thesis, University of Canterbury, Christchurch, New Zealand

Moder K, Moder K (2010) Alternatives to F-Test in One Way ANOVA in case of heterogeneity of variances (a simulation study). Psychological Test and Assessment Modeling 52 : 343–353

Moilanen A, Nieminen M (2002) Simple connectivity measures in spatial ecology. Ecology 83 : 1131–1145

Moilanen A, Van Teeffelen AJA, Ben-Haim Y, Ferrier S (2009) How much compensation is enough? A framework for incorporating uncertainty and time discounting when calculating offset ratios for impacted habitat. Restoration Ecology 17 : 470–478

Mokany K, Ash J, Roxburgh S (2008) Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. Journal of Ecology 96 : 884–893

Montoya D, Rogers L, Memmott J (2012) Emerging perspectives in the restoration of biodiversity-based ecosystem services. Trends in Ecology and Evolution 27 : 666–72

Moorhead LC, Philpott SM, Bichier P (2010) Epiphyte biodiversity in the coffee agricultural matrix: canopy stratification and distance from forest fragments. Conservation Biology 24 : 737–746

Moreno CE, Castillo-Campos G, Verdú JR (2009) Taxonomic diversity as complementary information to assess plant species diversity in secondary vegetation and primary tropical deciduous forest. Journal of Vegetation Science 20 : 935–943

Mori AS, Furukawa T, Sasaki T (2013) Response diversity determines the resilience of ecosystems to environmental change. Biological Reviews 88 : 349–64

Morris EK, Caruso T, Buscot F, Fischer M, Hancock C, Maier TS, … Rillig MC (2014) Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. Ecology and Evolution 4 : 3514–3524

Morrison EB, Lindell CA (2011) Active or passive forest restoration? Assessing restoration alternatives with avian foraging behavior. Restoration Ecology 19 : 170–177

Moser D, Zechmeister HG, Plutzar C, Sauberer N, Wrbka T, Grabherr G (2002) Landscape patch shape complexity as an effective measure for plant species richness in rural landscapes. Landscape Ecology 17 : 657–669

Mulongoy KJ, Chape S (Eds) (2004) Protected areas and biodiversity: an overview of key issues. CBD Secretariat and UNEP-WCMC, Montreal, Canada and Cambridge, UK.

Munro NT, Fischer J, Barrett G, Wood J, Leavesley A, Lindenmayer DB (2011) Bird's response to revegetation of different structure and floristics-are "restoration plantings" restoring bird communities? Restoration Ecology 19 : 223–235

Murphy DD, Weiland PS, Cummins KW (2011) A critical assessment of the use of surrogate species in conservation planning in the Sacramento-San Joaquin Delta, California (U.S.A.). Conservation Biology 25 : 873–878

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403 : 853–858

Nakamura A, Proctor H, Catterall CP (2003) Using soil and litter arthropods to assess the state of rainforest restoration. Ecological Management and Restoration 4 : 20–28

Neumann M, Starlinger F (2001) The significance of different indices for stand structure and diversity in forests. Forest Ecology and Management 145 : 91–106

Newton AC (2007) Forest structure and composition. Pages 85–146 In: Forest ecology and conservation: a handbook of techniques. Oxford University Press, Oxford, USA

Nijkamp P, Vindigni G, Nunes PALD (2008) Economic valuation of biodiversity:

a comparative study. Ecological Economics 67 : 217–231

Norton DA (2009a) Biodiversity offsets: two New Zealand case studies and an assessment framework. Environmental Management 43 : 698–706

Norton DA (2009b) Species invasions and the limits to restoration: learning from the New Zealand experience. Science 325 : 569–71

Norton DA, Miller CJ (2000) Some issues and options for the conservation of native biodiversity in rural New Zealand. Ecological Management and Restoration 1 : 26–34

Noss RF (1983) A regional landscape approach to maintain diversity. BioScience 33 : 700–706

Noss RF (1990) Indicators for monitoring biodiversity: a hierarchical approach. Conservation Biology 4 : 355–364

Noss RF (2000) High-risk ecosystems as foci for considering biodiversity and ecological integrity in ecological risk assessments. Environmental Science & Policy 3 : 321–332

Nuttle T, Hobbs RJ, Temperton VM, Halle S (2004) Assembly rules and ecosystem restoration: where to from here? Pages 410–421 In: Temperton VM, Hobbs RJ, Nuttle T, Halle S (eds) Assembly rules and restoration ecology: bridging the gap between theory and practice. Island Press, Washington D.C., USA

NZBOP (2012) Selection and weighting of attributes for use in biodiversity offsetting currencies. Contract report prepared by Wildland Consultants for New Zealand Biodiversity Offsets Programme, Department of Conservation, Wellington, New Zealand http://www.doc.govt.nz/documents/ conservation /biodiversity-offsetting-currencies.pdf

NZPCN (2016) New Zealand Plant Conservation Network (NZPCN) database. (available at: http://www.nzpcn.org.nz/page.aspx?flora).

O'Hara KL, Gersonde RF (2004) Stocking control concepts in uneven-aged silviculture. Forestry 77 : 131–143

Odum EP (1969) The strategy of ecosystem development. Science 164 : 262–270

Odum EP, Finn JT, Franz EH (1979) Perturbation theory and the subsidy-stress gradient. BioScience 29 : 349–352

Ogden J (1978) On the diameter growth rates of red beech (*Nothofagus fusca*) in different parts of New Zealand. New Zealand Journal of Ecology 1 : 16–18

Oksanen J, Friendly M, Blanchet FG, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2016) Vegan: community ecology package. (available from http://cran.r-project.org/package=vegan)

Oliver I, Beattie AJ (1996) Invertebrate morphospecies as surrogates for species: a case study. Conservation Biology 10 : 99–109

Oliver I, Eldridge DJ, Nadolny C, Martin WK (2014) What do site condition

multi-metrics tell us about species biodiversity? Ecological Indicators 38 : 262–271

Oliver I, Jones H, Schmoldt DL (2007) Expert panel assessment of attributes for natural variability benchmarks for biodiversity. Austral Ecology 32 : 453–475

Ostrowska A, Porębska G (2015) Assessment of the C/N ratio as an indicator of the decomposability of organic matter in forest soils. Ecological Indicators 49 : 104–109

Ottermanns R, Hopp PW, Guschal M, dos Santos GP, Meyer S, Roß-Nickoll M (2011) Causal relationship between leaf litter beetle communities and regeneration patterns of vegetation in the Atlantic rainforest of Southern Brazil (Mata Atlantica). Ecological Complexity 8 : 299–309

Paoletti MG, Osler GHR, Kinnear A, Black DG, Thomson LJ, Tsitsilas A, Sharley D, Judd S, Neville P, D'Inca A (2007) Detritivores as indicators of landscape stress and soil degradation. Australian Journal of Experimental Agriculture 47 : 412–423

Paquin P, Vink CJ, Dupérré N (2010) Spiders of New Zealand: annotated family key and species list. Manaaki Whenua Press, Lincoln, New Zealand

Parker GG, Brown MJ (2000) Forest canopy stratification-is it useful? The American Naturalist 155 : 473–484

Parkes D, Newell G, Cheal D (2003) Assessing the quality of native vegetation: the "habitat hectares" approach. Ecological Management & Restoration 4 : S29–S38

Parrotta JA, Knowles OH (1999) Restoration of tropical moist forests on bauxite-mined lands in the Brazilian Amazon. Restoration Ecology 7 : 103–116

Pascarella JB, Aide TM, Serrano MI, Zimmerman JK (2000) Land-use history and forest regeneration in the Cayey Mountains, Puerto Rico. Ecosystems 3 : 217–228

Pearce D, Moran D (1994) The economic value of biodiversity. Earthscan, London, UK

Pereira MJR, Marques JT, Palmeirim JM (2010) Vertical stratification of bat assemblages in flooded and unflooded Amazonian forests. Current Zoology 56 : 469–479

Perring MP, Standish RJ, Price JN, Craig MD, Erickson TE, Ruthrof KX, Whiteley AS, Valentine LE, Hobbs RJ (2015) Advances in restoration ecology: rising to the challenges of the coming decades. Ecosphere 6 : Article 131

Perry AD, Oren R, Hart SC (2008) The structure of local ecosystems. Forest structure. Pages 159–170 In: Forest ecosystems. The Johns Hopkins University Press, USA

Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. Ecology Letters 9 : 741–58

Peterson G, Allen CR, Holling CS (1998) Ecological resilience, biodiversity, and scale. Ecosystems 1 : 6–18

Piñeiro G, Oesterheld M, Batista WB, Paruelo JM (2006) Opposite changes of whole-soil vs. pools C:N ratios: a case of Simpson's paradox with implications on nitrogen cycling. Global Change Biology 12 : 804–809

Plourde BT, Boukili VK, Chazdon RL (2015) Radial changes in wood specific gravity of tropical trees: Inter- and intraspecific variation during secondary succession. Functional Ecology 29 : 111–120

Pommerening A (2002) Approaches to quantifying forest structures. Forestry 75 : 305–324

Pommerening A (2006) Evaluating structural indices by reversing forest structural analysis. Forest Ecology and Management 224 : 266–277

Pretzsch H (2009) Forest dynamics, growth and yield. Springer, Heidelberg, Berlin Germany

Prugh LR (2009) An evaluation of patch connectivity measures. Ecological Applications 19 : 1300–1310

Purvis A, Hector A (2000) Getting the measure of biodiversity. Nature 405 : 212–219

Quétier F, Lavorel S (2011) Assessing ecological equivalence in biodiversity offset schemes: key issues and solutions. Biological Conservation 144 : 2991–2999

Quétier F, van Teeffelen AJA, Pilgrim JD, von Hase A, ten Kate K (2015) Biodiversity offsets are one solution to widespread poorly compensated biodiversity loss: a response to Curran et al. Ecological Applications 25 : 1739–1741

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rands MRW, Adams WM, Bennun L, Butchart SHM, Clements A, Coomes D, Entwistle A, Hodge I, Kapos V, Scharlemann JPW, Sutherland WJ, Vira B (2010) Biodiversity conservation: challenges beyond 2010. Science 329 : 1298–1303

Rapport DJ, Whitford WG (1999) How ecosystems respond to stress. BioScience 49 : 193–203

Rayfield B, Anand M, Laurence S (2005) Assessing simple versus complex restoration strategies for industrially disturbed forests. Restoration Ecology 13 : 639–650

Reay SD, Norton DA (1999) Assessing the success of restoration plantings in a temperate New Zealand forest. Restoration Ecology 7 : 298–308

Revelle W (2015) psych: procedures for personality and psychological research. Version 1.5.1. Northwestern University, Evanston, Illinois, USA (available from http://cran.r-project.org/package=psych)

Rhoades CC, Eckert GE, Coleman DC (1998) Effect of pasture trees on soil

nitrogen and organic matter: implications for tropical montane forest restoration. Restoration Ecology 6 : 262–270

Richardson SJ, Laughlin DC, Lawes M, Holdaway R, Wilmshurst J, Wright M, Curran T, Bellingham PJ, McGlone M (2015) New Zealand tree bark thickness 2015. (available from https://datastore.landcareresearch.co.nz/dataset/new-zealand-bark-thickness-2015)

Rodgers DJ, Kitching RL (1998) Vertical stratification of rainforest collembolan (Collembola:Insecta) assemblages: description of ecological patterns and hypotheses concerning their generation. Ecography 21 : 392–400

Rodrigues ASL, Brooks TM (2007) Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. Annual Review of Ecology, Evolution, and Systematics 38 : 713–737

Roe D, Hollands M (2004) Protected areas: how much is enough? Parks Magazine 14 : 42–44

Roque F de O, Guimarães EA, Ribeiro MC, Escarpinati SC, Suriano MT, Siqueira T (2014) The taxonomic distinctness of macroinvertebrate communities of Atlantic Forest streams cannot be predicted by landscape and climate variables, but traditional biodiversity indices can. Brazilian Journal of Biology 74 : 991–999

Rouvinen S, Kuuluvainen T (2005) Tree diameter distributions in natural and managed old *Pinus sylvestris*-dominated forests. Forest Ecology and Management 208 : 45–61

Ruiz-Jaén MC, Aide TM (2005a) Restoration success: how is it being measured? Restoration Ecology 13 : 569–577

Ruiz-Jaén MC, Aide TM (2005b) Vegetation structure, species diversity, and ecosystem processes as measures of restoration success. Forest Ecology and Management 218 : 159–173

Ryndock JA, Stratton GE, Brewer JS, Holland MM (2012) Differences in spider community composition among adjacent sites during initial stages of oak woodland restoration. Restoration Ecology 20 : 24–32

Salmon S, Geoffroy JJ, Ponge JF (2005) Earthworms and collembola relationships: effects of predatory centipedes and humus forms. Soil Biology and Biochemistry 37 : 487–495

Salzman J, Ruhl JB (2000) Currencies and the commodification of environmental law. Stanford Law Review 53 : 607–693

Sanders HL (1968) Marine benthic diversity: a comparative study. The American Naturalist 102 : 243–282

Saunders A, Norton DA (2001) Ecological restoration at Mainland Islands in New Zealand. Biological Conservation 99 : 109–119

Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5 : 18–32

Saura S, Carballal P (2004) Discrimination of native and exotic forest patterns through shape irregularity indices: an analysis in the landscapes of Galicia, Spain. Landscape Ecology 19 : 647–662

Saura S, Torras O, Gil-Tena A, Pascual-Hortal L (2008) Shape irregularity as an indicator of forest biodiversity and guidelines for metric selection. Pages 167–189 In: Lafortezza R, Chen J, Sanesi G, Crow TR (eds) Patterns and processes in forest landscapes: multiple use and sustainable management. Springer Netherlands, New York , USA

Schlesinger WH (1984) Soil organic matter: a source of atmospheric CO2. Pages 111–127 In: Woodwell GM (ed) The role of terrestrial vegetation in the global carbon cycle: measurement by remote sensing. SCOPE 23. John Wiley & Sons Ltd, New York, USA

Schleuter D, Daufresne M, Massol F, Argillier C (2010) A user's guide to functional diversity indices. Ecological Monographs 80 : 469–484

Schloter M, Dilly O, Munch JC (2003) Indicators for evaluating soil quality. Agriculture, Ecosystems and Environment 98 : 255–262

Schoonmaker P, McKee A (1988) Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. Forest Science 34 : 960–979

Schulze CH, Linsenmair KE, Fiedler K (2001) Understorey versus canopy: patterns of vertical stratification and diversity among Lepidoptera in a Bornean rain forest. Plant Ecology 153 : 133–152

Secretariat of the Convention on Biological Diversity (2010) Global biodiversity outlook 3. (Vol. 69)Montreal, Canada

Secretariat of the Convention on Biological Diversity (CBD) (2005) Handbook of the convention on biological diversity including its Cartagena protocol on biosafety (3rd ed.)Montreal, Canada

Shackelford N, Hobbs RJ, Burgar JM, Erickson TE, Fontaine JB, Laliberté E, Ramalho CE, Perring MP, Standish RJ (2013) Primed for change: developing ecological restoration for the 21st century. Restoration Ecology 21 : 297–304

Shannon CE (1948) A mathematical theory of communication. The Bell System Technical Journal 27 : 623–656

Simmonds SJ, Majer JD, Nichols OG (1994) A comparative study of spider (Araneae) communities of rehabilitated bauxite mines and surrounding forest in the southwest of Western Australia. Restoration Ecology 2 : 247–260

Simpson EH (1949) Measurement of diversity. Nature 163 : 688

Six J, Jastrow JD (2006) Organic matter turnover. Pages 1210–1215 In: Lal R (ed) Encyclopedia of soil science. Volume 2. Taylor & Francis, New York, USA

Smale MC, Hall GM, Gardner RO (1995) Dynamics of kanuka (*Kunzea ericoides*) forest on South Kaipara Spit, New Zealand, and the impact of fallow deer

(*Dama dama*). New Zealand Journal of Ecology 19 : 131–141

Smale MC, Kimberley MO (1993) Regeneration patterns in montane conifer/broadleaved forest on Mt Pureora, New Zealand. New Zealand Journal of Forestry Science 23 : 123–141

Smith B, Wilson JB (1996) A consumer' s guide to evenness indices. Oikos 76 : 70–82

Snyder BA, Hendrix PF (2008) Current and potential roles of soil macroinvertebrates (earthworms, millipedes, and isopods) in ecological restoration. Restoration Ecology 16 : 629–636

Society for Ecological Restoration International Science & Policy Working Group (2004) The SER international primer on ecological restoration. http://www.ser.org/resources/resources-detail-view/ser-international-primer-on-ecological-restoration

Solid Energy New Zealand Limited (2009) BBOP pilot project case study. Strongman Mine. Business and Biodiversity Offsets Programme (BBOP), Christchurch, New Zealand http://bbop.forest-trends.org/guidelines/index.php

Spake R, Ezard THG, Martin PA, Newton AC, Doncaster CP (2015) A meta-analysis of functional group responses to forest recovery outside of the tropics. Conservation Biology 29 : 1695–1703

Spellerberg IF (2005) Diversity and similarity indices. Pages 191–219 In: Monitoring ecological change. Cambridge University Press, New York, USA

Spies TA (1998) Forest structure: a key to the ecosystem. Northwest Science 72 : 34–39

Spies TA, Franklin JF (1988) Old growth and forest dynamics in the Douglas-fir region of Western Oregon and Washington. Nat. Areas J. 8 : 190–201

Spies TA, Franklin JF (1991) The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. Pages 91–110 In: Ruggiero LF, Aubry KB, Carey AB, Huff MH (eds) Wildlife and vegetation of unmanaged Douglas-fir forests. General Technical Report PNW-GTR-285. U.S. Department of Agriculture, Forest Service, Portland, USA

Srivastava DS, Cadotte MW, MacDonald AAM, Marushia RG, Mirotchnick N (2012) Phylogenetic diversity and the functioning of ecosystems. Ecology Letters 15 : 637–648

Srivastava DS, Vellend M (2005) Biodiversity-ecosystem function research: is it relevant to conservation? Annual Review of Ecology, Evolution, and Systematics 36 : 267–294

Standish RJ, Hobbs RJ, Mayfield MM, Bestelmeyer BT, Suding KN, Battaglia LL, Eviner V, Hawkes C V, Temperton VM, Cramer VA, Harris JA, Funk JL, Thomas PA (2014) Resilience in ecology: abstraction, distraction, or where the action is? Biological Conservation 177 : 43–51

Stansbury CD (2001) Dispersal of the environmental weed Bridal Creeper,

Asparagus asparagoides, by Silvereyes, *Zosterops lateralis*, in south-western Australia. Emu 101 : 39–45

Staudhammer CL, LeMay VM (2001) Introduction and evaluation of possible indices of stand structural diversity. Canadian Journal of Forest Research 31 : 1105–1115

Stevenson BA (2004) Changes in phosphorus availability and nutrient status of indigenous forest fragments in pastoral New Zealand Hill country. Plant and Soil 262 : 317–325

Stirling G, Wilsey B (2001) Empirical relationships between species richness, evenness, and proportional diversity. The American Naturalist 158 : 286–299

Strickland MS, Lauber C, Fierer N (2009) Testing the functional significance of microbial community composition. Ecology 90 : 441–451

Strickland MS, Osburn E, Lauber C, Fierer N, Bradford MA (2009) Litter quality is in the eye of the beholder: initial decomposition rates as a function of inoculum characteristics. Functional Ecology 23 : 627–636

Sturtevant BR, Bissonette JA, Long JN, Roberts DW (1997) Coarse woody debris as a function of age, stand structure, and disturbance in Boreal Newfoundland. Ecological Applications 7 : 702–712

Suding KN (2011) Toward an era of restoration in ecology: successes, failures, and opportunities ahead. Annual Review of Ecology, Evolution, and Systematics 42 : 465–87

Suding KN, Hobbs RJ (2009) Threshold models in restoration and conservation: a developing framework. Trends in Ecology and Evolution 24 : 271–279

Suganuma MS, Durigan G (2015) Indicators of restoration success in riparian tropical forests using multiple reference ecosystems. Restoration Ecology 23 : 238–251

Sullivan JJ, Williams PA, Timmins SM (2007) Secondary forest succession differs through naturalised gorse and native kānuka near Wellington and Nelson. New Zealand Journal of Ecology 31 : 22–38

Swanson ME, Franklin JF, Beschta RL, Crisafulli CM, Dellasala DA (2011) The forgotten stage of forest succession: early-successional ecosystems on forest sites.

Tabarelli M, Peres CA, Melo FPL (2012) The "few winners and many losers" paradigm revisited: emerging prospects for tropical forest biodiversity. Biological Conservation 155 : 136–140

Temperton VM, Hobbs RJ (2004) The search for ecological assembly rules and its relevance to restoration ecology. Pages 34–54 In: Temperton VM, Hobbs RJ, Nuttle T, Halle S (eds) Assembly rules and restoration ecology: bridging the gap between theory and practice. Island Press, Washington D.C., USA

ten Kate K, Bishop J, Bayon R (2004) Biodiversity offsets: views, experience, and the business case. IUCN and UK and Insight Investment, Gland,

Switzerland and Cambridge, London, UK https://www.biodiv.org/doc/case-studies/inc/cs-inc-IUCN-II-report-en.pdf

Tierney GL, Faber-Langendoen D, Mitchell BR, Shriver WG, Gibbs JP (2009) Monitoring and evaluating the ecological integrity of forest ecosystems. Frontiers in Ecology and the Environment 7 : 308–316

Tischendorf L, Bender DJ, Fahrig L (2003) Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. Landscape Ecology 18 : 41–50

Tollefson J (2011) Seven billion and counting. Nature 478 : 300–300

Treweek J (1999) Ecological impact assessment. Blackwell Science Ltd., Malden, USA

Tripathi KP, Singh B (2005) The role of revegetation for rehabilitation of sodic soils in semiarid subtropical forest, India. Restoration Ecology 13 : 29–38

Tucker CM, Cadotte MW, Carvalho SB, Davies TJ, Ferrier S, Fritz SA, Grenyer R, Helmus MR, Jin LS, Mooers AO, Pavoine S, Purschke O, Redding DW, Rosauer DF, Winter M, Mazel F (2016) A guide to phylogenetic metrics for conservation, community ecology and macroecology. Biological Reviews doi:10.1111/brv.12252 (in press)

Tuomisto H (2012) An updated consumer's guide to evenness and related indices. Oikos 121 : 1203–1218

Uetz GW (1979) The influence of variation in litter habitats on spider communities. Oecologia 40 : 29–42

Uetz GW (1990) Habitat structure and spider foraging. Pages 325–348 In: Bell SS, McCoy ED, Mushinsky HR (eds) Habitat structure: The physical arrangement of objects in space. Volume 8 of the series: population and community biology. Chapman and Hall, New York , USA

UNEP (2007) Global environment outlook. United Nations Environment Programme. (Vol. GEO 4)Nairobi, Kenya

United Nations (2011) The millennium development goals report 2011. UNO, New York , USA

United Nations Environment Programme (1992) Convention on biological diversity. United Nations Environment Programme, Nairobi, Kenya https://www.cbd.int/doc/legal/cbd-en.pdf

Valbuena R, Packalén P, Martín-Fernández S, Maltamo M (2012) Diversity and equitability ordering profiles applied to study forest structure. Forest Ecology and Management 276 : 185–195

van Andel J, Grootjans AP, Aronson J (2012) Unifying concepts. Pages 9–22 In: Van Andel J, Aronson J (eds) Restoration ecology: the new frontier. Wiley-Blackwell, West Sussex, UK

Van Den Meerssehaut, Diego Vandekerkhove K (2000) Development of a stand-scale forest biodiversity index based on the state forest inventory. Pages 340–349 In: Hansen M, Burk T (eds) Integrated tools for natural resources

inventories in the 21st century. USDA, Boise, USA

Van Straalen NM, Verhoef HA (1997) The development of a bioindicator system for soil acidity based on arthropod pH preferences. Journal of Applied Ecology 34 : 217–232

Vandekerkhove K, De Keersmaeker L, Menke N, Meyer P, Verschelde P (2009) When nature takes over from man: dead wood accumulation in previously managed oak and beech woodlands in North-western and Central Europe. Forest Ecology and Management 258 : 425–435

Varga P, Chen HYH, Klinka K (2005) Tree-size diversity between single- and mixed-species stands in three forest types in western Canada. Canadian Journal of Forest Research 35 : 593–601

Vellend M, Cornwell WK, Magnuson-Ford K, Mooers AØ (2011) Measuring phylogenetic biodiversity. Pages 194–207 In: Magurran AE, McGill B (eds) Biological diversity: frontiers in measurement and assessment. Oxford University Press, New York, USA

Vesk P a., Nolan R, Thomson JR, Dorrough JW, Nally R Mac (2008) Time lags in provision of habitat resources through revegetation. Biological Conservation 141 : 174–186

Villéger S, Mason NWH, Mouillot D, Mason H (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89 : 2290–2301

Vivanco L, Austin AT (2008) Tree species identity alters forest litter decomposition through long-term plant and soil interactions in Patagonia, Argentina. Journal of Ecology 96 : 727–736

von Euler F, Svensson S (2001) Taxonomic distinctness and species richness as measures of functional structure in bird assemblages. Oecologia 129 : 304–311

Wake DB, Vredenburg VT (2008) Are we in the midst of the sixth mass extinction? A view from the world of amphibians. Proceedings of the National Academy of Sciences of the United States of America 105 : 11466–11473

Walker LR, Wardle DA, Bardgett RD, Clarkson BD (2010) The use of chronosequences in studies of ecological succession and soil development. Journal of Ecology 98 : 725–736

Walker S, Brower AL, Stephens RTT, Lee WG (2009) Why bartering biodiversity fails. Conservation Letters 2 : 149–157

Wall DH, Bradford MA, St. John MG, Trofymow JA, Behan-Pelletier V, Bignell DE, … Zou X (2008) Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. Global Change Biology 14 : 2661–2677

Wallwork JA (1970) Ecology of soil animals. McGraw-Hill, London, UK

Ward DF, Larivière MC (2004) Terrestrial invertebrate surveys and rapid

biodiversity assessment in New Zealand: Lessons from Australia. New Zealand Journal of Ecology 28 : 151–159

Ward JB, Macfarlane RP, Quinn PJ, Morris SJ, Hitchings TR, Green EH, … Wilson HD (1999) Insects and other arthropods of Hinewai Reserve, Banks Peninsula, New Zealand. (Vol. 13). Records of the Canterbury Museum, Christchurch, New Zealand

Ward SC, Majer JD, O'Connell AM (1991) Decomposition of eucalypt litter on rehabilitated bauxite mines. Austral Ecology 16 : 251–257

Wardle DA (2002) Communities and ecosystems. Linking the aboveground and belowground components. Princeton University Press, Princeton, USA

Wardle DA (2006) The influence of biotic interactions on soil biodiversity. Ecology Letters 9 : 870–886

Wardle DA (2009) Aboveground and belowground consequences of long-term forest retrogression in the timeframe of millennia and beyond. Pages 193–209 In: Wirth C, Gleixner G, Heimann M (eds) Old-growth forests. Function, fate and value. Springer-Verlag, Berlin, Heidelberg, Germany

Wardle DA, Bardgett RD, Klironomos JN, Setälä H, van der Putten WH, Wall DH (2004) Ecological linkages between aboveground and belowground biota. Science 304 : 1629–33

Wardle DA, Barker GM, Yeates GW, Bonner KI, Ghani A (2001) Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. Ecological Monographs 71 : 587–614

Wardle DA, Yeates GW, Barker GM, Bonner KI (2006) The influence of plant litter diversity on decomposer abundance and diversity. Soil Biology and Biochemistry 38 : 1052–1062

Wardle JA (1984) Forest disturbances associated with climate, geology and fire. Pages 146–173 In: The New Zealand beeches. Ecology, utilisation and management. New Zealand Forest Service, Wellington, New Zealand

Wardle JA (1984) Stand structure and growth. Pages 296–326 In: The New Zealand beeches. Ecology, utilisation and management. N.Z. Forest Service,Caxton Press, Christchurch, New Zealand

Wardle P (2002) Vegetation of New Zealand. The Blackburn Press, Caldwell, USA

Warwick RM (2008) Average taxonomic diversity and distinctness. Pages 300–305 In: Jorgensen SE, Fath B (eds) Encyclopedia of ecology. Elsevier B.V., Amsterdam, The Netherlands

Warwick RM, Clarke KR (1995) New "biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. Marine Ecology Progress Series 129 : 301–305

Warwick RM, Clarke KR (1998) Taxonomic distinctness and environmental assessment. Journal of Applied Ecology 35 : 532–543

Watts CH, Gibbs GW (2002) Revegetation and its effect on the ground-dwelling

beetle fauna of Matiu-Somes Island, New Zealand. Restoration Ecology 10 : 96–106

Wei T (2013) corrplot: Visualization of a correlation matrix. R package version 0.73. (available from http://cran.r-project.org/package=corrplot)

Welch ABL (1947) The generalization of `Student's' problem when several different population variances are involved. Biometrika 34 : 28–35

Wells JA (1972) Ecology of *Podocarpus hallii* in Central Otago, New Zealand. New Zealand Journal of Botany 10 : 399–426

White E, Tucker N, Meyers N, Wilson J (2004) Seed dispersal to revegetated isolated rainforest patches in North Queensland. Forest Ecology and Management 192 : 409–426

White PS, Jentsch A (2004) Disturbance, succession, and community assembly in terrestrial plant communities. Pages 341–366 In: Temperton VM, Hobbs RJ, Nuttle T, Halle S (eds) Assembly rules and restoration ecology: bridging the gap between theory and practice. Island Press, USA, Washington, D.C.

Willett TR (2001) Spiders and other arthropods as indicators in old-growth versus logged Redwood stands. Restoration Ecology 9 : 410–420

Williams PA, Karl BJ (1996) Fleshy fruits of indigenous and adventive plants in the diet of birds in forest remnants, Nelson, New Zealand. New Zealand Journal of Ecology 20 : 127–145

Wilson HD (1988) The botany of Hinewai Reserve. Journal of the Canterbury Botanical Society 22 : 18–30

Wilson HD (1990) Gorse on Hinewai Reserve. Journal of the Canterbury Botanical Society 24 : 45–47

Wilson HD (1993) Bioclimatic Zones and Banks Peninsula. Journal of the Canterbury Botanical Society 24 : 22–29

Wilson HD (1994) Regeneration of native forest on Hinewai Reserve, Banks Peninsula. New Zealand Journal of Botany 32 : 373–383

Wilson HD (1998) Living in Raoul country: the changing flora and vegetation of Banks Peninsula. Pages 101–121 In: Burrows CJ (ed) Etienne Raoul and Canterbury botany 1840–1996. Canterbury Botanical Society and Manuka Press, Christchurch, New Zealand

Wilson HD (2003) Nature not nurture; minimum interference management and forest restoration on Hinewai reserve, Banks Peninsula. Canterbury Botanical Society Journal 37 : 25–41

Wiser SK, Bellingham PJ, Burrows LE (2001) Managing biodiversity information: development of New Zealand's National Vegetation Survey databank. New Zealand Journal of Ecology 25 : 1–17

Wodika BR, Klopf RP, Baer SG (2014) Colonization and recovery of invertebrate ecosystem engineers during prairie restoration. Restoration Ecology 22 : 456–464

Wortley L, Hero J-M, Howes M (2013) Evaluating ecological restoration success: a review of the literature. Restoration Ecology 21 : 537–543

Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proceedings of the National Academy of Sciences of the United States of America 96 : 1463–1468

Young TP (2000) Restoration ecology and conservation biology. Biological Conservation 92 : 73–83

Zak DR, Grigal DF, Gleeson S, Tilman D (1990) Carbon and nitrogen cycling during old-field succession: constraints on plant and microbial biomass. Biogeochemistry 11 : 111–129

Zenner EK, Hibbs DE (2000) A new method for modeling the heterogeneity of forest structure. Forest Ecology and Management 129 : 75–87

Zeppelini D, Bellini BC, Creão-Duarte AJ, Hernández MIM (2009) Collembola as bioindicators of restoration in mined sand dunes of northeastern Brazil. Biodiversity and Conservation 18 : 1161–1170

Ziesche TM, Roth M (2008) Influence of environmental parameters on small-scale distribution of soil-dwelling spiders in forests: what makes the difference, tree species or microhabitat? Forest Ecology and Management 255 : 738–752

Zuur AF, Ieno EN, Smith GM (2007) Analysising ecological data. (Statistics for Biology and Health) (M. Gail, K. Krickeberg, J. Samet, A. Tsiatis, & W. Wong, Eds.). Springer Science, New York, London

Appendix 1

Summarizing constancy table, providing the frequency for the dominant woody species in each successional stage (i.e.). Values shown are calculated for the 'Species Importance' data set.

	Successional stage	Species	Frequency of occurrence
Mixed-broadleaved forest	Pasture	-	-
	Gorse	*Ulex europeus*	1
	Emergent natives	*Ulex europeus*	1
		Melicytus ramiflorus	0.667
		Fuchsia excorticata	0.6
		Aristotelia serrata	0.533
	Fuchsia dominated-mixed-broadleaved forest	*Fuchsia excorticata*	1
		Melicytus ramiflorus	0.75
		Aristotelia serrata	0.65
		Schefflera digitata	0.65
	Māhoe-dominated mixed-broadleaved forest	*Melicytus ramiflorus*	1
		Fuchsia excorticata	0.636
Kānuka forest	Early kānuka forest	*Kunzea robusta*	1
	Intermediate kānuka forest	*Kunzea robusta*	1
		Pseudowintera colorata	0.473684
		Schefflera digitata	0.315789
	Late kānuka forest	*Kunzea robusta*	1
		Schefflera digitata	0.846154
		Fuchsia excorticata	0.615385
		Melicytus ramiflorus	0.615385
		Pseudopanax colensoi	0.615385
		Pseudowintera colorata	0.615385
Reference	Old growth forest	*Fuscospora fusca*	1
		Pseudopanax crassifolius	0.364
		Podocarpus laetus	0.318

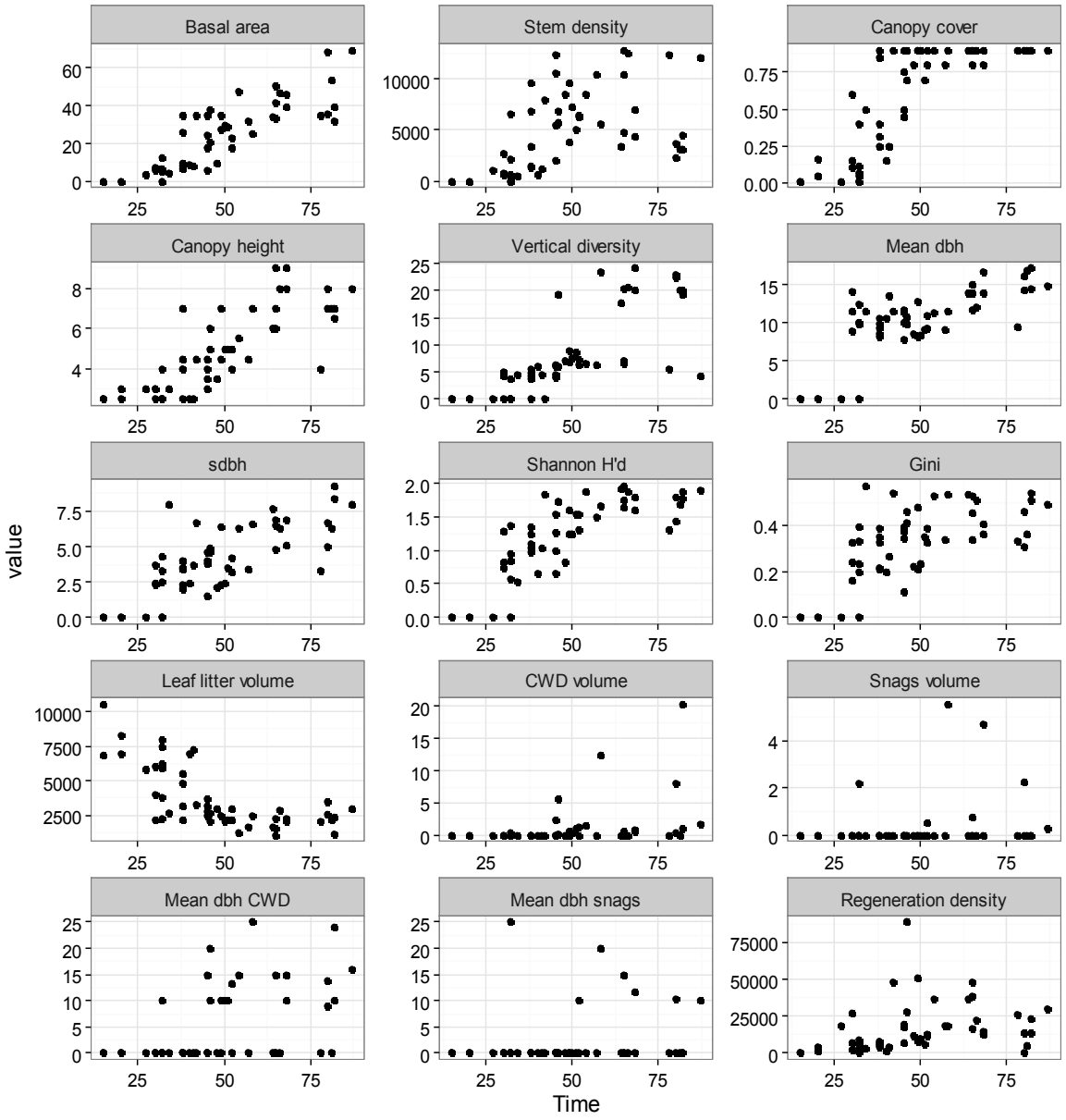
Appendix 2

Regression results for structural attribute development in kānuka and the mixed-broadleaved trajectory over increasing recovery time. Data transformation applied are indicated for y (attribute) and x (time), model terms used for the predictor are denoted. The slope was standardized and calculated without any transformations for comparability reasons.

	Attributes	*Units*	R^2	*F*	*DF*	*p*	*slope*	transf.		model terms
								y	x	
Kanuka forest	Gini coefficient	index	0.60	60.2	1,41	<0.001	0.027	log		linear
	Canopy cover	%	0.32	19.8	1,41	<0.001	-0.029	logit		quadratic
	Shannon *H'd*	index	0.65	74.7	1,41	<0.001	0.029	log		linear
	Vertical diversity	index	0.67	86	1,41	<0.001	0.028			linear
	Basal area	m^2/ha^{-1}	0.53	46.7	1,40	0.0377	0.035			linear
	Stem density	stems/ha	0.7	66.5	1,29	<0.001	-0.029	log		linear
	Canopy height	m	0.82	188.3	1,41	<0.001	0.032		log	linear
	Mean dbh	cm	0.69	91.7	1,41	<0.001	0.028	log	log	linear
	s_{dbh}	cm	0.8	167.5	1,41	<0.001	0.030	log		linear
	Leaf litter volume	m^3	0.13	6	1,41	0.0191	-0.012			linear
	CWD volume	m^3/ha^{-1}	0.19	9.4	1,41	0.0038	0.015	lin		linear
	Mean diameter CWD	cm	0.28	15.8	1,41	0.0003	0.0180	lin		linear
	Snags volume	m^3/ha^{-1}	0.54	47.9	1,41	<0.001	0.016	log	log	linear
	Mean diameter snags	cm	0.62	66.8	1,41	<0.001	0.025			linear
	Regeneration density	$count/ha^{-1}$	0.17	6.3	1,31	0.0179	0.0110	log		linear
Broadleaved forest	Gini coefficient	index	0.50	51.3	1,51	<0.001	0.035		log	linear
	Canopy cover	%	0.70	59.2	2,50	<0.001	0.042	logit		quadratic
	Shannon *H'd*	index	0.68	105.9	1,51	<0.001	0.042		log	linear
	Vertical diversity	index	0.54	60.5	1,51	<0.001	0.038		log	linear
	Basal area	m^2/ha^{-1}	0.72	131.5	1,51	<0.001	0.054			linear
	Stem density	stems/ha	0.50	21.8	2,44	<0.001	0.028			quadratic
	Canopy height	m	0.70	119.2	1,50	<0.001	0.043			linear
	Mean dbh	cm	0.53	28.4	2,50	<0.001	0.039			quadratic
	s_{dbh}	cm	0.56	65.6	1,51	<0.001	0.041			liniear
	Leaf litter volume	m^3	0.57	32.6	2,50	<0.001	-0.036			quadratic
	CWD volume	m^3/ha^{-1}	0.26	18.4	1,51	<0.001	0.020	log		linear
	Mean diameter CWD	cm	0.37	29.4	1,51	<0.001	0.026			linear
	Snags volume	m^3/ha^{-1}	0.04	2.2	1,51	0.14	-			linear
	Mean diameter snags	cm	0.04	2.2	1,51	0.15	-			linear
	Regeneration density	$count/ha^{-1}$	0.13	7.7	1,51	0.008	0.017	log		linear

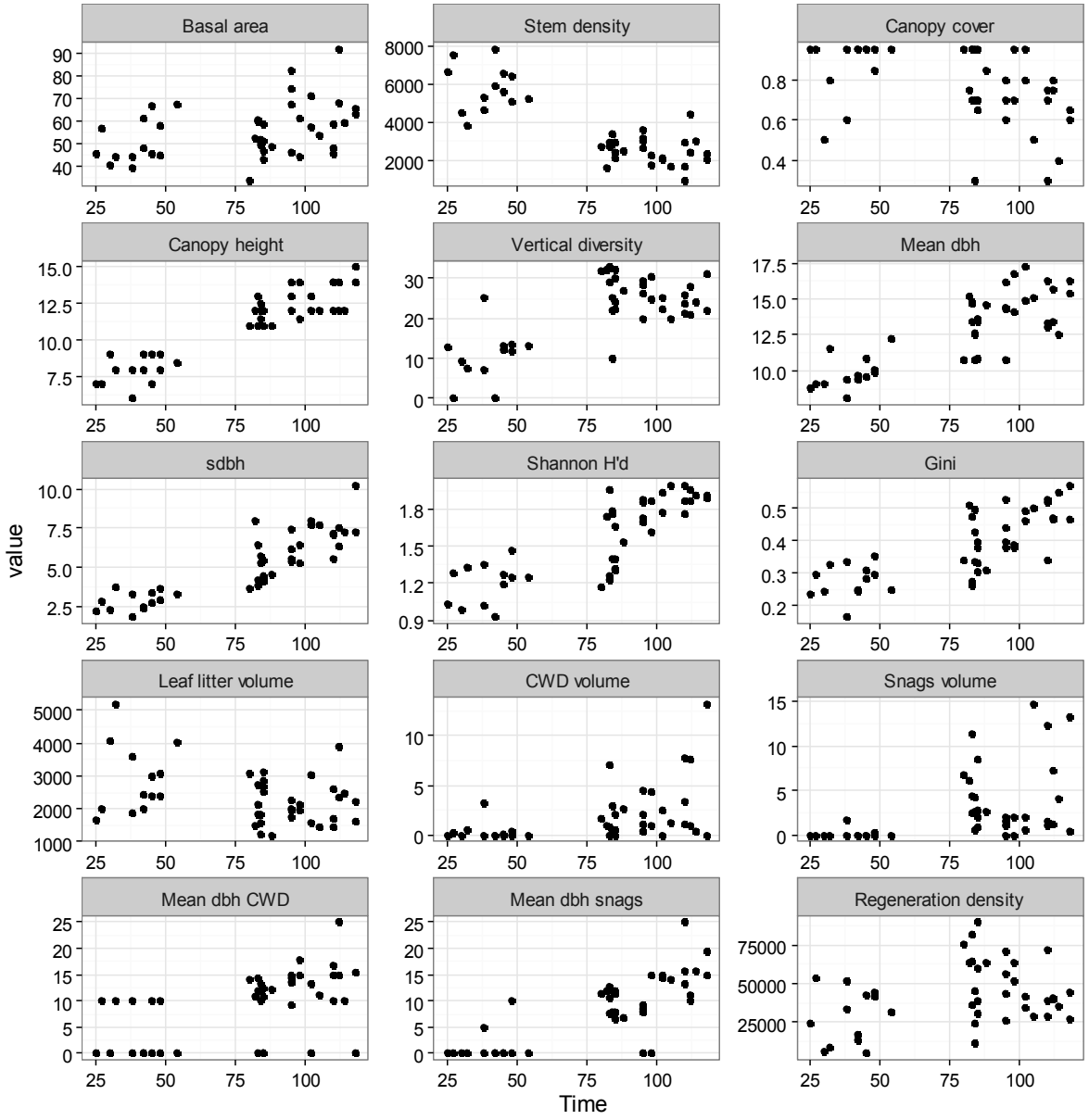
Appendix 3

Scatterplots showing the behaviour of all tested structural variables over increasing recovery time for the mixed-broadleaved trajectory. For units used and regression model results see Appendix 2. Raw data without transformation is displayed.



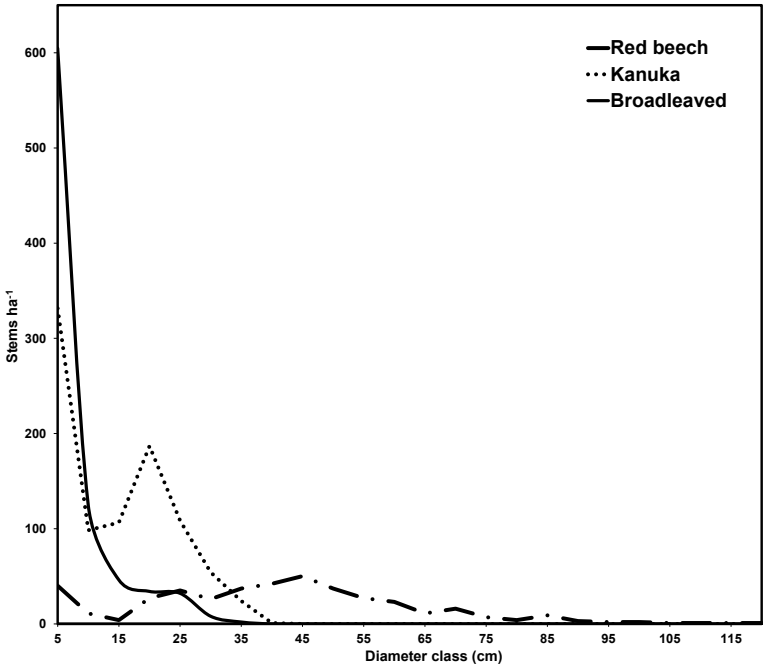
Appendix 4

The development of all investigated structural attributes over increasing recovery time is shown for the kānuka trajectory in the scatterplots below. Raw data without transformation is depicted. See Appendix 2 for attribute units and linear model results.



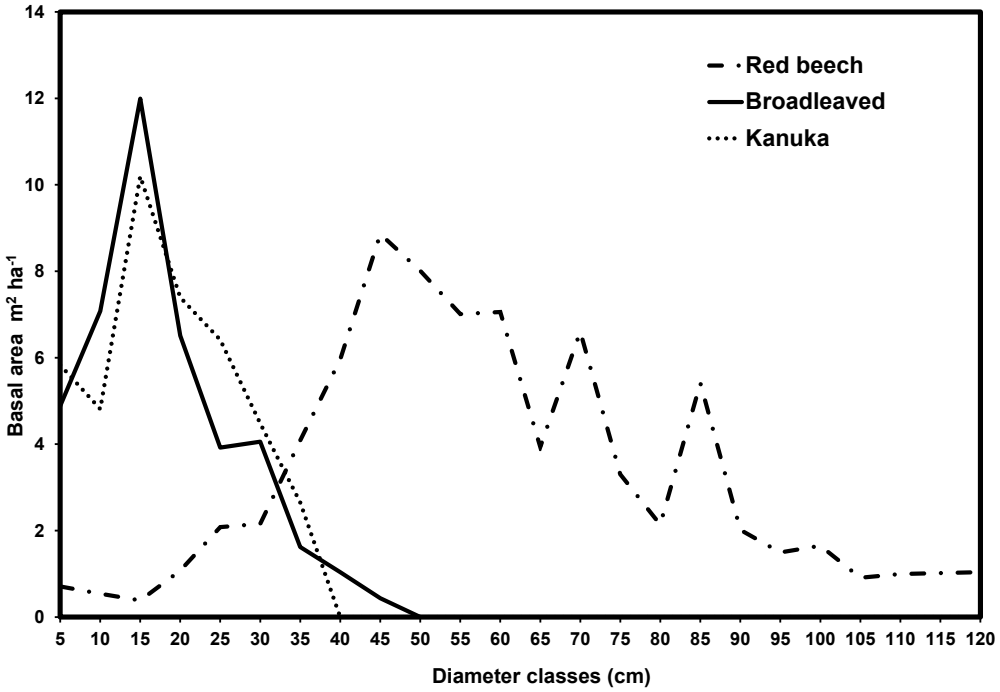
Appendix 5

Diameter distribution for the oldest 15 percent of the two second growth forests (kānuka and mixed-broadleaved) and the reference sites (red beech forest). The lower limits of the diameter classes are depicted (bin size 5 cm).



Appendix 6

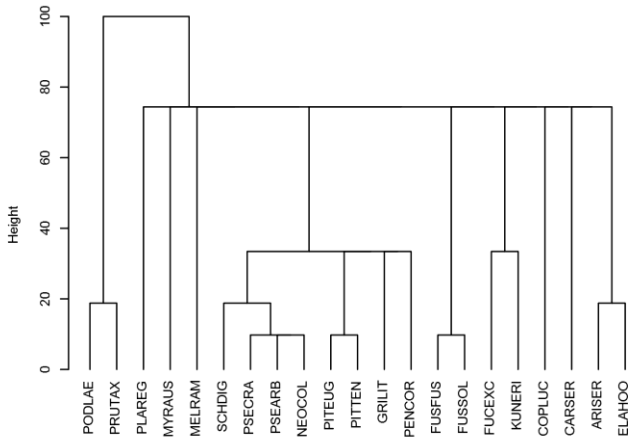
Average basal area distribution per diameter class for all forest types using the oldest 15 percent of the second growth forests.



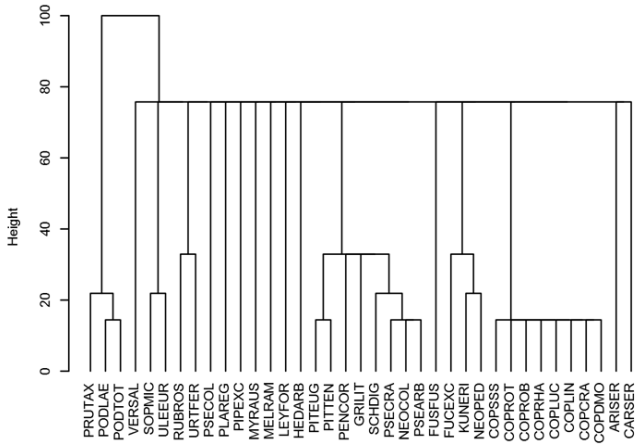
Appendix 7

Taxonomic trees based on five levels of taxonomic classification (species, genus, family, order, class) used for calculation of taxonomic indices for the tree (A), shrub (B) and fern (C) tiers. Species code abbreviations and the correspondent scientific plant names are provided in Appendix 9.

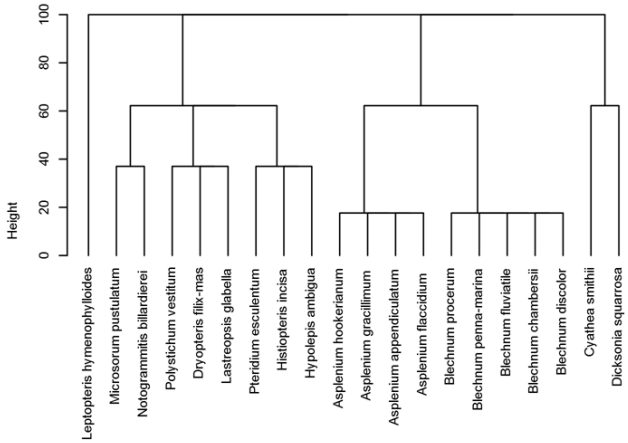
A



B

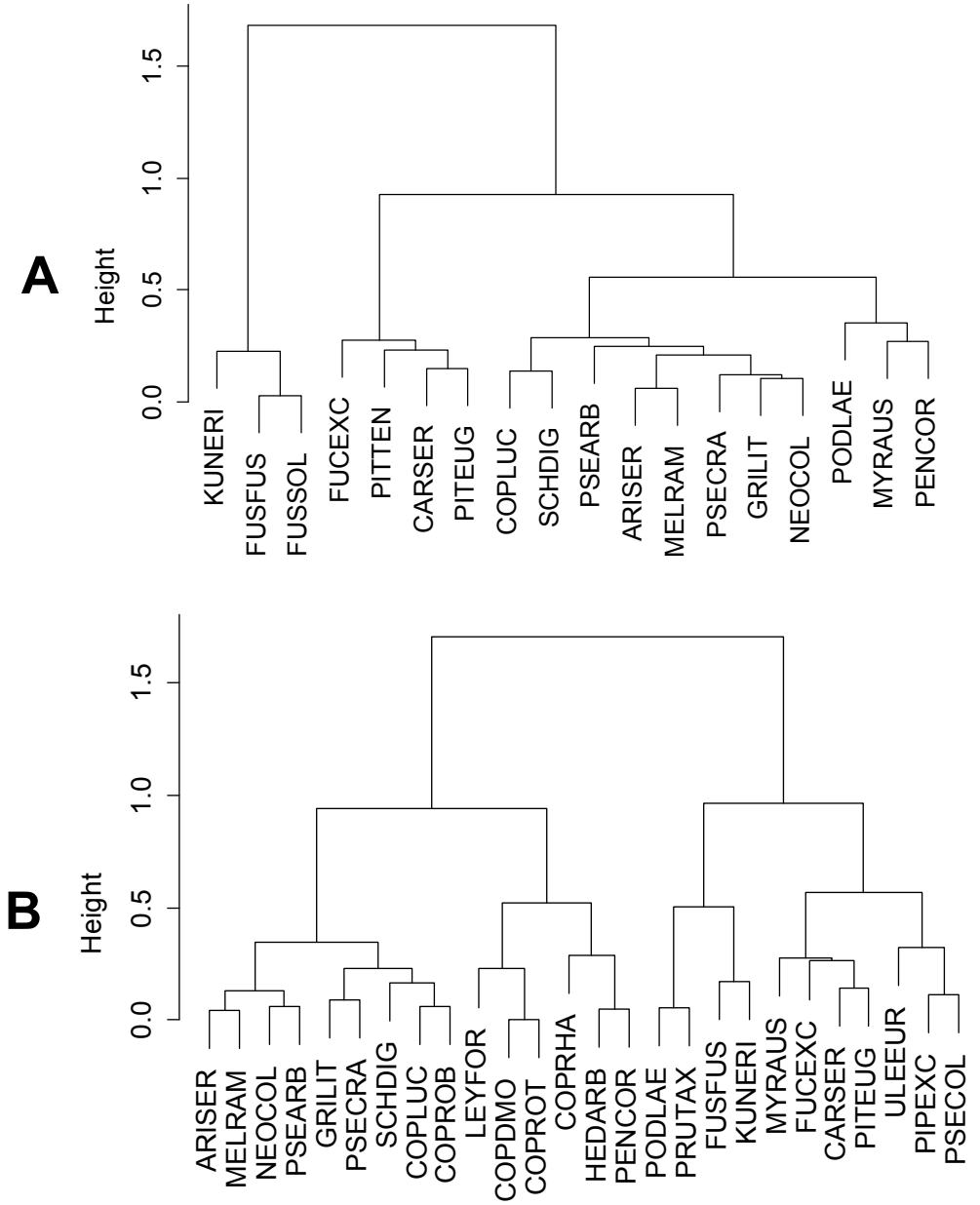


C



Appendix 8

Functional dendrograms used for calculating functional group richness for the tree (A) and shrub (B) layer. Hierarchical cluster analysis on Euclidean distance matrices was used to group species according to their functional similarity. The following plant traits were chosen as input data: *fruit size*, *type of seed dispersal*, *mode of reproductive organs*, *life mode*, *leaf mass per area*, *resprouting ability*, *palatability* and *leaf width.* Taxonomic species names for species codes used can be found Appendix 9.



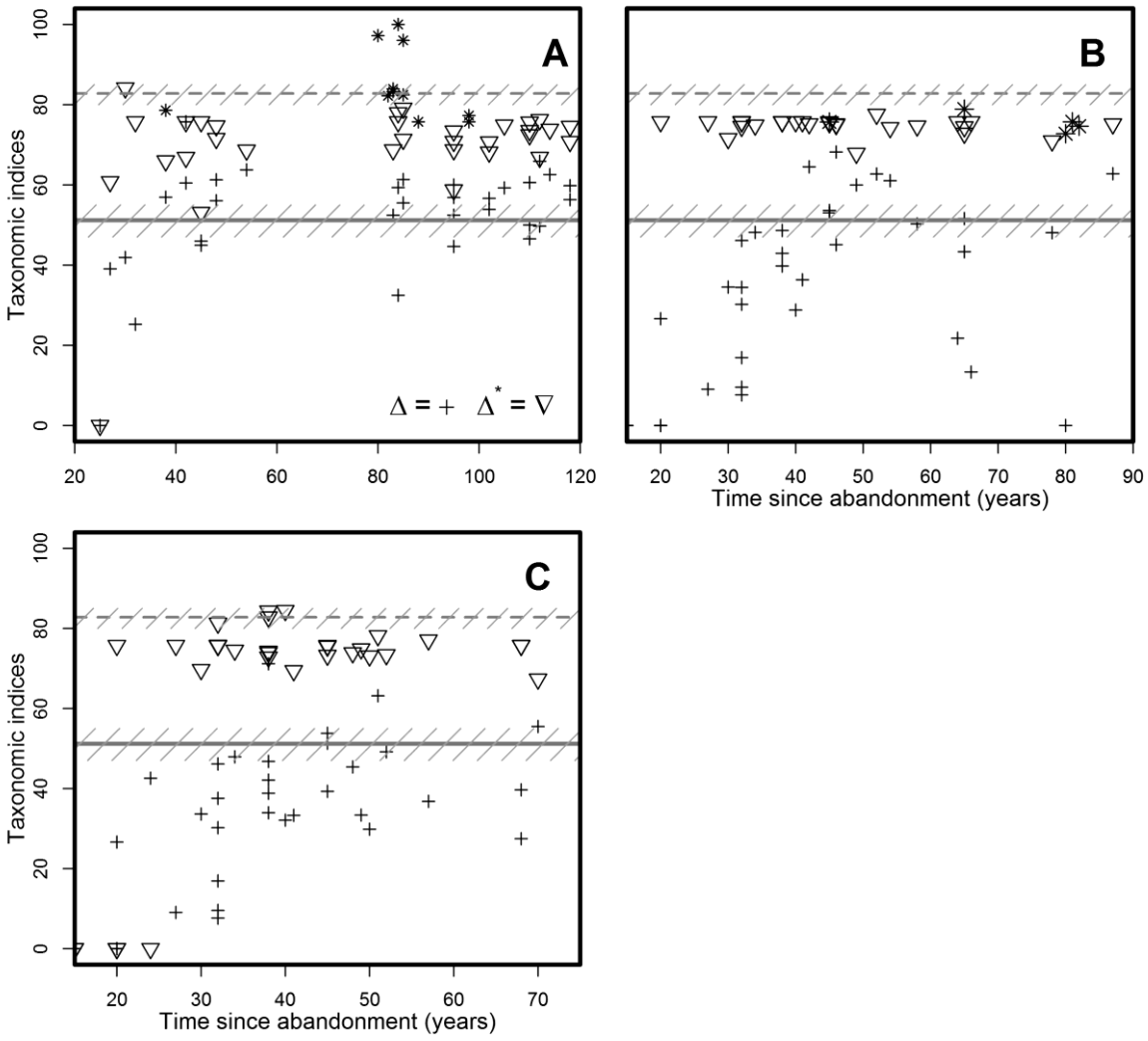
Appendix 9

Woody species abbreviations employed for the functional and taxonomic dendrograms, following the codes used in the New Zealand National Vegetation Survey Databank (NVS), available at https://nvs.landcareresearch.co.nz /Resources/NVSNames.

Species	Species code
Aristotelia serrata	ARISER
Carpodetus serratus	CARSER
Coprosma crassifolia	COPCRA
Coprosma dumosa	COPDMO
Coprosma linariifolia	COPLIN
Coprosma lucida	COPLUC
Coprosma propinqua	COPPRO
Coprosma rhamnoides	COPRHA
Coprosma robusta	COPROB
Coprosma rotundifolia	COPROT
Elaeocarpus hookerianus	ELAHOO
Fuchsia excorticata	FUCEXC
Fuscospora fusca	FUSFUS
Fuscospora solandri	FUSSOL
Griselinia littoralis	GRILIT
Hebe salicifolia	VERSAL
Hedycarya arborea	HEDARB
Kunzea ericoides	KUNERI
Leycesteria formosa	LEYFOR
Piper excelsum	PIPEXC
Melicytus ramiflorus	MELRAM
Myrsine australis	MYRAUS
Neomyrtus pedunculata	NEOPED
Pennantia corymbosa	PENCOR
Pittosporum eugenioides	PITEUG
Pittosporum tenuifolium	PITTEN
Plagianthus regius	PLAREG
Podocarpus laetus	PODLAE
Podocarpus totara	PODTOT
Prumnopitys taxifolia	PRUTAX
Pseudopanax arboreus	PSEARB
Pseudopanax colensoi	NEOCOL
Pseudopanax crassifolius	PSECRA
Pseudowintera colorata	PSECOL
Rubus fruticosus	RUBROS
Schefflera digitata	SCHDIG
Sophora microphylla	SOPMIC
Ulex europeus	ULEEUR
Urtica ferox	URTFER

Appendix 10

Taxonomic index results for individual sampling plots are displayed over estimated plot age. Values for Δ (cross) and Δ* (triangle) are given for the shrub tier for **(A)** kānuka, **(B)** fuchsia, **(C)** māhoe vegetation trajectories within Hinewai Reserve. Stars (Δ*) are representing still grazed plots, outside of Hinewai. The shaded area and lines are indicating reference forest values. The dashed line represents the taxonomic distinctness (Δ*) the solid line depicts mean 'average taxonomic diversity' (Δ), and the shaded area is respectively giving the SE of the mean.



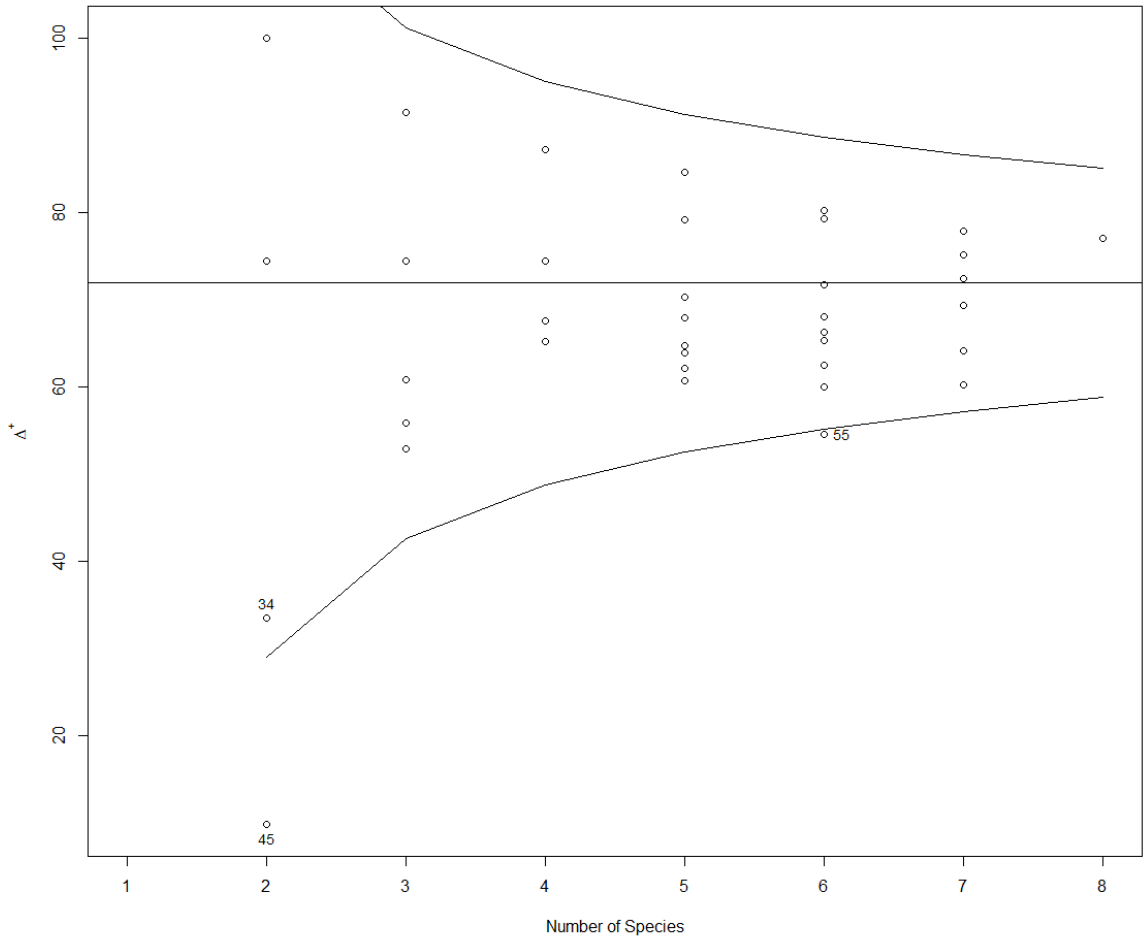
Appendix 11

Results for standard linear regression models, investigating relationship of biodiversity attributes with increasing recovery time. Appropriate data transformation was applied and is denoted in 'trans'. Standardised slope values are given.

	Fuchsia						Mahoe						Kanuka					
					trans.						trans.						trans.	
	Slope	R^2	*p* value	DF	y	x	Slope	R^2	*p* value	DF	y	x	Slope	R^2	*p* value	Df	y	x
Shannon (tr)	0.025	0.52	<0.001	38		log	0.070	0.14	0.050	32		log	0.031	0.50	<0.001	30	log	log
Simpson (tr)	0.021	0.50	<0.001	39		log	0.020	0.06	0.200	32		log	0.018	0.38	<0.001	30	log	log
Evenness (tr)	-0.024	0.23	0.004	32	logit		-0.047	0.35	<0.001	32		logit	-0.012	0.00	0.960	30	logit	
Species richness (tr)	0.033	0.57	<0.001	39		log	0.051	0.56	<0.001	32		log	0.022	0.50	<0.001	30		
Shannon (sh)	0.016	0.25	0.008	39	log	log	0.036	0.42	<0.001	32		log	0.020	0.49	<0.001	30	log	log
Simpson (sh)	0.015	0.22	<0.001	39	log	log	0.030	0.30	<0.001	32	log	log	0.016	0.25	<0.001	30		
Evenness (sh)	-0.010	0.01	0.430	32	logit		-0.027	0.15	0.024	32	logit		-0.018	0.31	<0.001	28	logit	
Species richness (sh)	0.015	0.17	0.007	39	log	log	0.040	0.41	<0.001	32		log	0.025	0.61	<0.001	30		
Shannon (fer)	0.021	0.19	0.002	39		log	0.034	0.28	<0.001	32		log	0.004	0.01	0.597	30		
Simpson (fer)	0.014	0.11	0.047	39		log	0.027	0.16	0.004	32		log	0.002	0.00	0.774	30		
Evenness (fer)	-0.035	0.58	<0.001	37	logit		-0.048	0.45	<0.001	32	logit		-0.010	0.11	0.060	30	logit	
Species richness (fer)	0.036	0.58	<0.001	39			0.047	0.46	<0.001	32			0.010	0.10	0.074	30		
Species richness (total)	0.033	0.56	<0.001	39		log	0.035	0.18	0.011	32	log	log	0.026	0.64	<0.001	31	log	log
tax. Delta (tr)	0.020	0.18	0.010	32		log	0.016	0.55	0.549	32		log	0.023	0.53	<0.001	31		log
tax. Delta* (tr)	0.014	0.35	0.760	32		log	0.022	0.15	0.152	32			0.019	0.37	<0.001	31		
tax. Lambda+ (tr)	0.026	0.54	<0.001	32			0.026	0.15	0.152	32			0.013	0.39	<0.001	30		
tax. Delta (sh)	0.019	0.29	<0.001	34		log	0.042	0.46	0.459	32		log	0.012	0.00	0.965	30		log
tax. Delta* (sh)	-0.006	0.01	0.656	34			0.014	0.07	0.068	32			0.010	0.10	0.060	30		
tax. Lambda+ (sh)	0.013	0.05	0.060	35			0.020	0.06	0.058	32			0.004	0.10	0.060	30		
tax. Delta (fer)	0.010	0.10	0.080	37			0.027	0.20	0.201	31			0.000	0.00	0.790	30		
tax. Delta* (fer)	0.023	0.23	<0.001	37			0.034	0.23	0.230	32			0.002	0.01	0.668	30		
tax. Lambda+ (fer)	0.030	0.39	<0.001	37			0.051	0.52	0.519	32			0.016	0.27	0.002	30		
tax. Lambda+ (total)	0.007	0.03	0.265	37			0.009	0.02	0.021	32			-0.007	0.03	0.323	30		
tax. Delta+ (total)	0.009	0.01	0.597	39			0.020	0.11	0.113	32			-0.006	0.06	0.165	30		
Dispersal (bird%)	0.036	0.66	<0.001	39	logit		0.058	0.75	<0.001	32	logit		0.021	0.43	<0.001	30	logit	
Dispersal (wind%)	0.010	0.00	0.993	39	logit		0.004	0.02	0.462	32	logit		-0.021	0.41	<0.001	30	logit	
Dispersal (gravity%)	-0.038	0.82	<0.001	39	logit		-0.057	0.72	<0.001	32	logit		-0.009	0.07	0.146	30	logit	
GF (medium trees%)	0.033	0.63	<0.001	39	logit		0.057	0.73	<0.001	32	logit		0.017	0.34	<0.001	30	logit	
GF (shrubs %)	-0.034	0.61	<0.001	39	logit		-0.056	0.68	<0.001	32	logit		0.015	0.47	<0.001	30	logit	
GF (small trees%)	0.003	0.10	0.090	39	logit		0.004	0.01	0.570	32	logit		0.010	0.13	0.041	30	logit	
GF (large trees later%)	-0.007	0.04	0.229	39	logit		0.025	0.07	0.126	32	logit		0.011	0.11	0.060	30	logit	
GF (large trees early%)	0.017	0.10	0.010	39	logit		0.009	0.05	0.205	32	logit		-0.021	0.43	<0.001	30	logit	
Fric (tr)	0.031	0.31	0.009	19	log		-0.008	0.03	0.622	11	log		0.018	0.22	0.032	19	log	
Fdiv (tr)	0.007	0.01	0.618	29	logit		-0.013	0.03	0.590	11	logit		-0.012	0.09	0.188	19	logit	
RaoQ (tr)	0.020	0.16	0.020	32		log	-0.001	0.01	0.720	25			0.023	0.52	0.321	30		
Fdis (tr)	0.025	0.25	0.002	32		log	0.005	0.01	0.574	25			0.023	0.51	<0.001	30		
Feve (tr)	0.006	0.01	0.627	19	logit		-0.008	0.01	0.700	11	logit		0.027	0.17	<0.001	19	logit	
FGR (tr)	0.035	0.47	<0.001	32	log	log	0.038	0.24	0.010	25			0.022	0.49	<0.001	30		
FGR (sh)	0.016	0.12	0.029	39			0.049	0.48	<0.001	32			0.025	0.65	<0.001	30		
Fric (sh)	0.002	0.01	0.531	32			0.001	0.24	0.580	25			0.019	0.34	<0.001	27		
Fdiv (sh)	-0.015	0.12	0.061	19	logit		-0.037	0.23	0.011	25	logit		-0.003	0.01	0.687	27	logit	
RaoQ (sh)	0.006	0.06	0.115	39			0.019	0.01	0.640	32			0.017	0.33	<0.001	30		
Fdis (sh)	0.010	0.12	0.026	39			0.025	0.21	0.006	32			0.018	0.39	<0.001	30		
Fev (sh)	0.005	0.01	0.586	29	logit		0.003	0.01	0.620	25	logit		-0.011	0.16	0.030	27	logit	

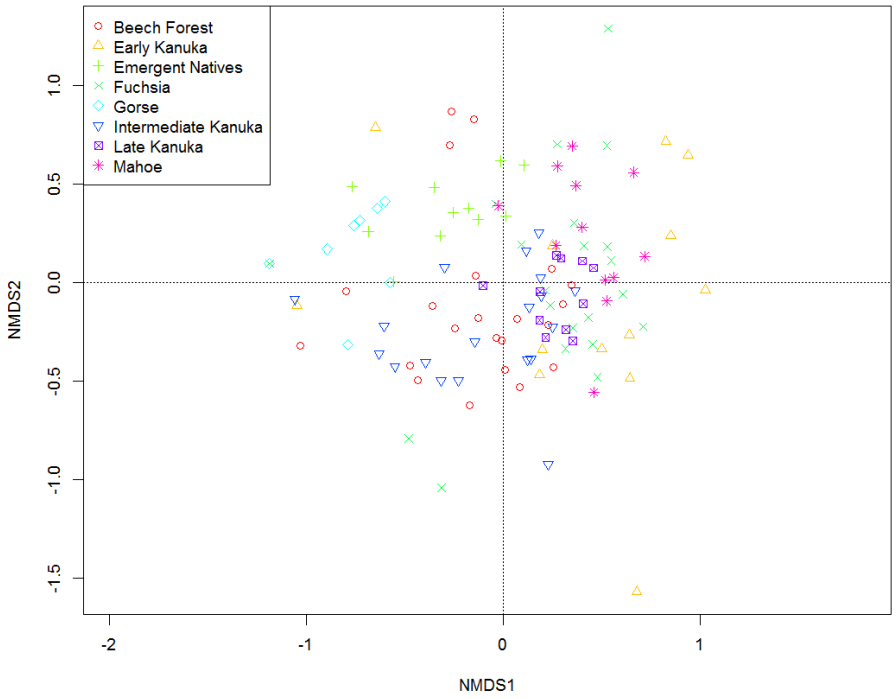
Appendix 12

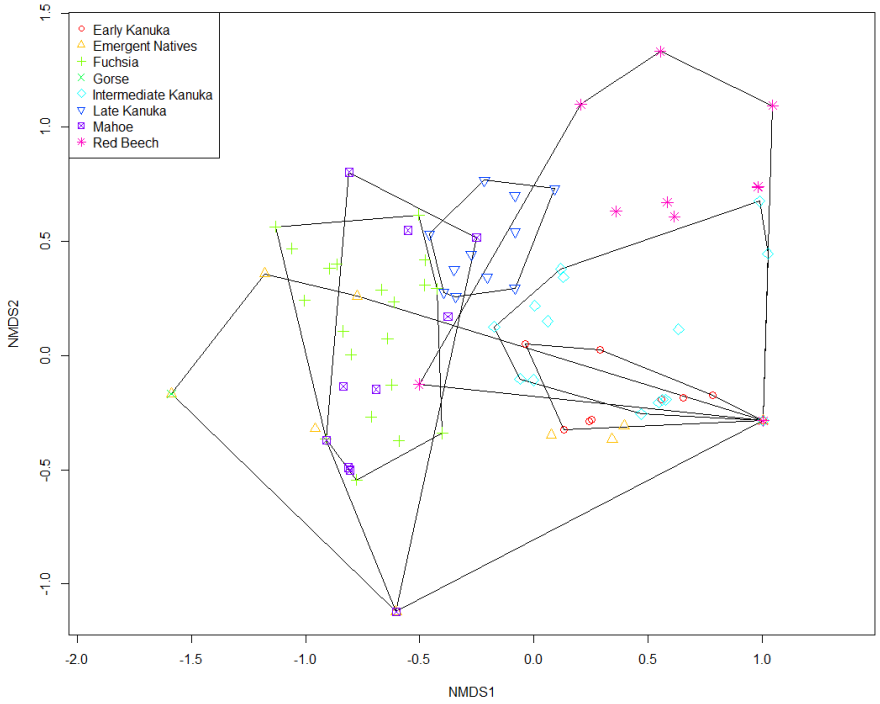
Average taxonomic distinctness Δ^+ (circles) for the tree tier across all sampling plots/trajectories, the solid line indicates the expected taxonomic distinctness which was calculated taking random subsamples and the 95% probability limits for a single Δ^+ value (funnel) to be observed.



Appendix 13

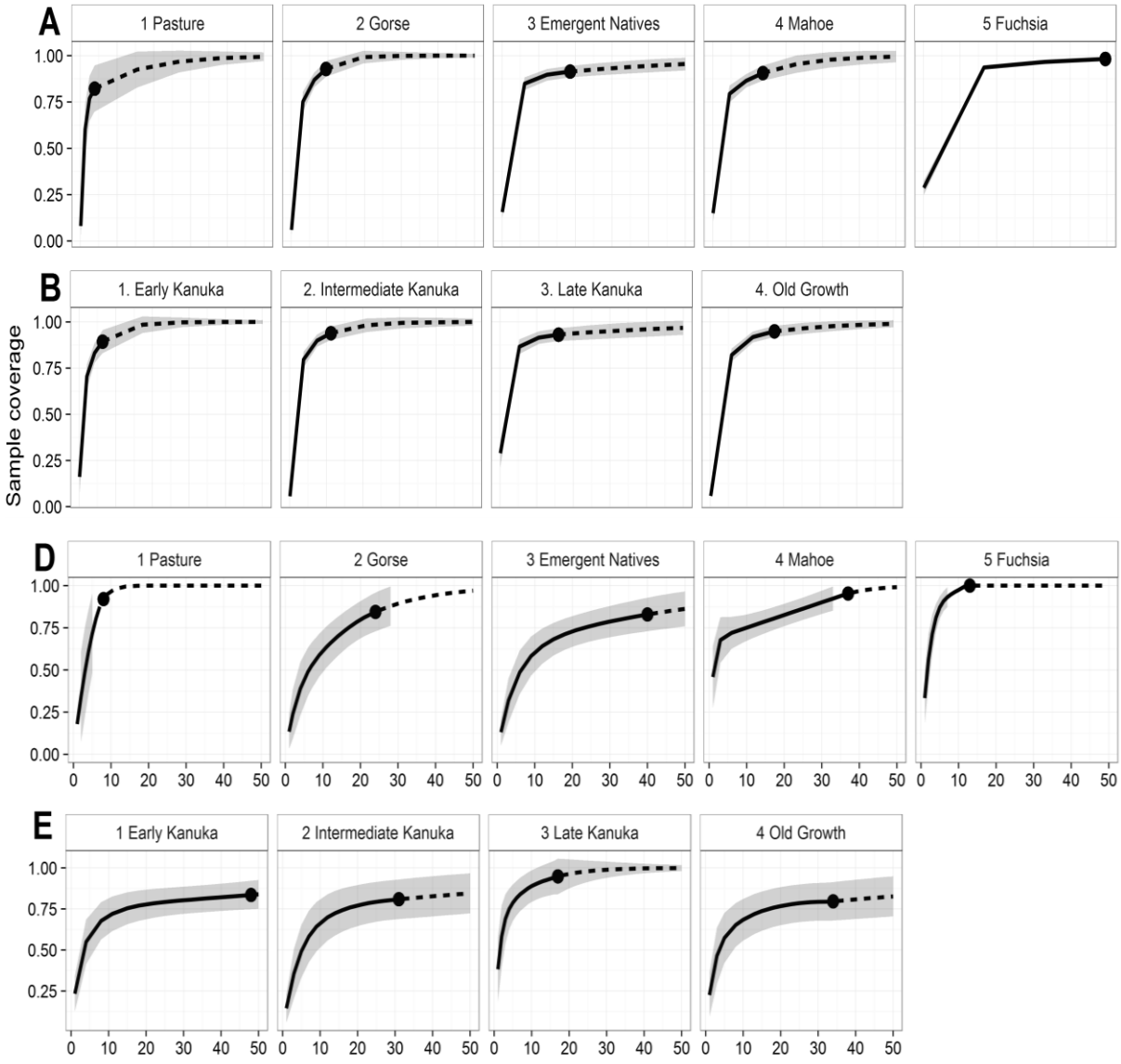
NMDS ordinations on abundances per functional group for the shrub (A) and the tree (B) tier. The functional group data set gained by cluster analysis was used (Appendix 8). Bray–Curtis dissimilarity was applied for both ordinations, convergent solutions were found (shrub= stress: 0.20, tree = Stress: 0.13).





Appendix 14

Sample completeness curves for beetle (A-B) and spider (D-E) species (RTUs) over increasing individuals sampled for all vegetation types within the two main forest trajectories (A, D = mixed-broadleaved forest, B, E = kānuka forest). Observed values (solid lines) and 95 % CIs of extrapolated sample coverage (shaded area) are given for 200 replications using bootstrapping. Calculations are based on methods described by Chao et al. (2014).



Appendix 15

Number of RTUs identified from each family of adult beetles, millipedes, and centipedes collected. Millipedes and centipedes were considered in the data analysis to represent the diversity of decomposers and predators respectively. Beetles were analysed as a taxa containing a range of functional groups and therefore representative of invertebrate diversity more generally.

Beetles				Millipedes		Centipedes	
Family	n	Family	n	Family	n	Family	n
Aderidae	1	Lateridiidae	1	Iulomorphidae	1	Chilenophilidae	1
Anthribidae	2	Latridiidae	1	Dalodesmidae	5	Geophilidae	1
Bothrideridae	1	Leiodidae	1	Haplodesmidae	1	Henicopidae	4
Brentidae	1	Mordellidae	1	Metopidiotrichidae	3	Triaenonychidae	1
Byrrhidae	2	Mycetophagidae	2	Siphonophoridae	1		
Cantharidae	1	Ptiliidae	3	Siphonotidae	1		
Carabidae	5	Scarabaeidae	2	Total	12	Total	7
Cerambycidae	4	Scydmaenidae	1				
Chrysomelidae	1	Staphylinidae	15				
Cryptophagidae	2	Tenebrionidae	1				
Curculionidae	17	Trogossitidae	1				
Elateridae	1	Zopheridae	5				
Entiminae	1	Total	72				

Appendix 16

NMDS plots on Bray-Curtis dissimilarity for the decomposer communities (all invertebrates belonging to this group) in the kānuka (below) and mixed-broadleaved (above) trajectories. Convergent solutions were found for both plots, stress level were 0.22 (mixed-broadleaved) and 0.25 (kānuka).